Dinopedia

A Brief Compendium of Dinosaur Lore

Darren Naish

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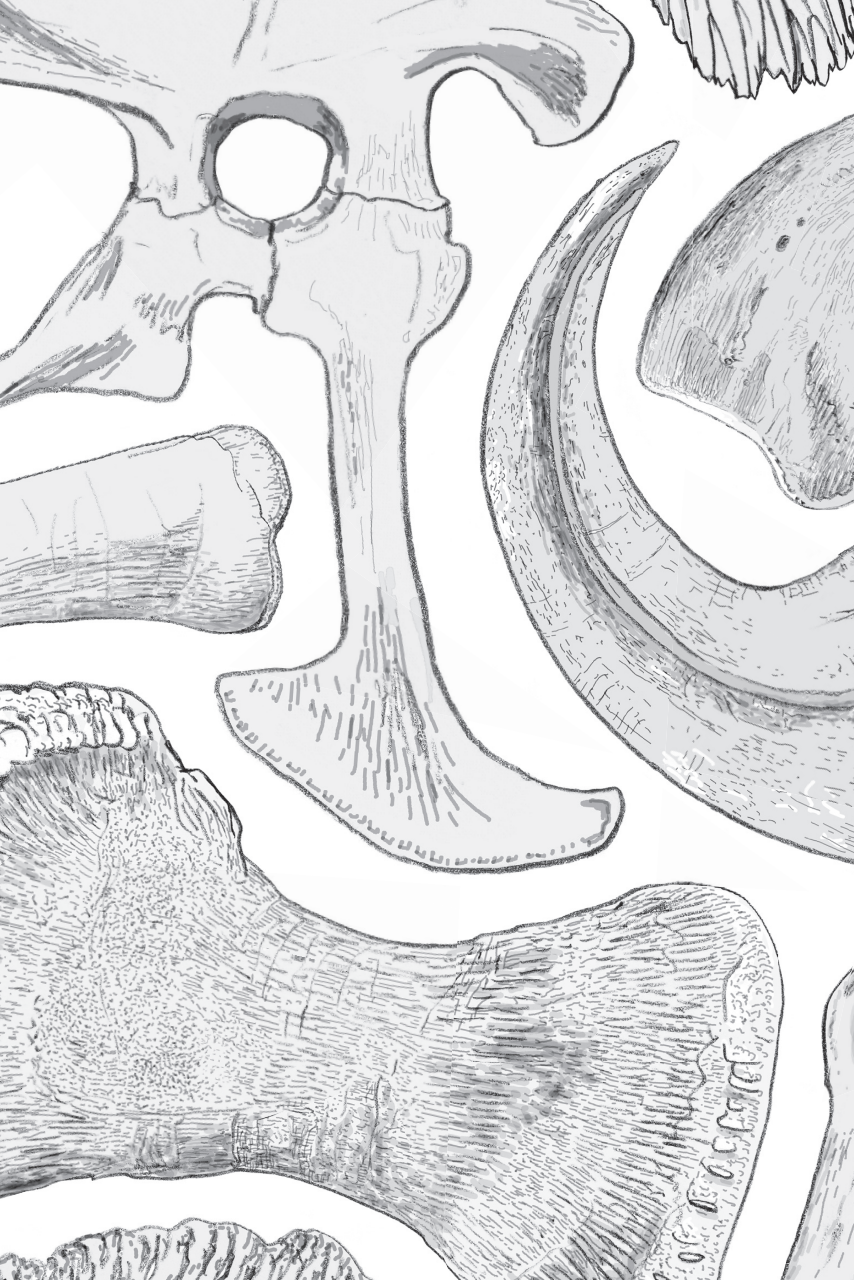

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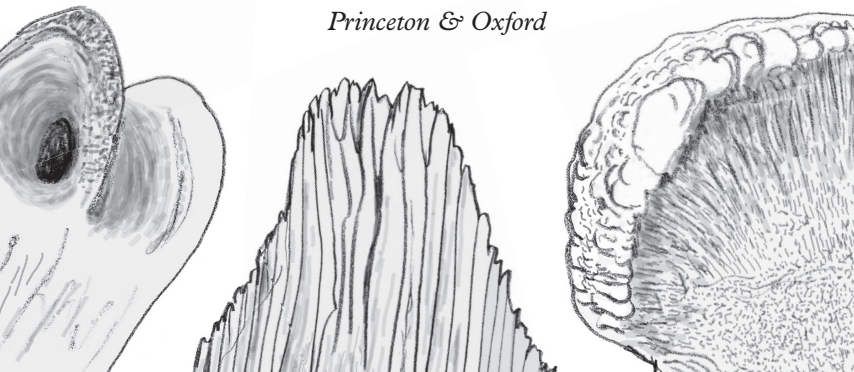

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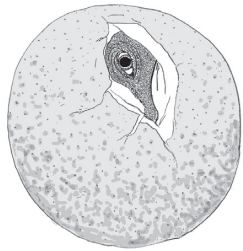


Preface

For a group of animals that died out 65.5 million years ago, dinosaurs (well: *non-bird dinosaurs* . . . read on) have a remarkable grip on our imagination. And despite claims that things have waxed and waned with the popularity of certain movie franchises or TV shows, my strong impression as someone with a long-term involvement in dinosaur-themed books, exhibits, popular writing, and scientific research is that this interest is a permanent and steady fixture, and it isn't going away.

Why does this connection to dinosaurs exist? I think it's complex, and not easy to summarize. But I'll try. Yes, dinosaurs were often big, and many people are awed by them because of their perceived fierceness, size, or vague similarity to mythic archetypes like dragons. But they were also *animals*, animals with sleek lines, streamlined, aesthetically interesting faces, bodies decorated with frills, spikes, and other ornaments, with muscular arms sporting meathook-like claws, and great column-like legs. This combination of features makes dinosaurs

of many sorts appealing, neat-looking animals, at least as fascinating as big cats, bears, Komodo dragons, giant fishes, or whales (all animals to which humans also have a demonstrable attraction). Here's the base tier of my argument: we like dinosaurs because, frankly, they're neat-looking animals.

Yet dinosaurs go *beyond* the neat-looking, attractive living animals that so often hold our attention. Because, you see, *dinosaurs were super animals*. You don't have to be a paleontologist, anatomist, or qualified scientist of any sort to look at the skeleton of a sauropod, a *Triceratops*, or a *Tyrannosaurus* and realize that this animal is *off the charts*. The giant, typically long legs of these animals show that they were swift, muscular, and powerful, built something like super-charged giant mammals or great birds yet with a reptilian veneer. The form of the neck and skull demonstrates an active air, acute senses, and a capacity for finding and demolishing food. And the massive size of the body cavity, the size, depth, and width of the shoulder and hip girdles, is surely linked to the presence of a giant metabolic powerhouse for those great jaws, enormous limbs, and muscular tail. Bears, tigers, giant crocodiles, Komodo dragons, elephants, and rhinos are all fantastic, but—I'll say it again—dinosaurs are simply *phenomenal*, way beyond the most awesome of living animals, way beyond anything we can experience in the modern world. Ok, the great whales might come close, but they—obviously—are animals of the oceanic realm, not the land. This is the second tier of my argument: we like dinosaurs because they're *super animals*, above and beyond living creatures when it comes to mechanics, power, and abilities.

In the modern world, those great animals—big cats, crocodiles, elephants, and the other creatures I've mentioned—are in trouble. Their world is shrinking as we cannot help but take it from them; they are few and becoming fewer. Most of us know this, are sad for it, and struggle to imagine these creatures having a bright future. The animals of the deep geological past of course inhabited a human-free world, and thinking of them as living creatures not only removes any guilt, sadness, or concern we might have; it also allows us to consider the vast wildernesses they were part of. This is the third tier of my argument. I think that people of all sorts have an inherent fascination with truly wild landscapes, with the concept of an unbroken, natural frontier; a wilderness unspoilt by human action. The fact that these spectacular, awesome animals massed in great herds, fought over mating rights, killed, ate, hunted, mated, survived, thrived, grew, lived and died in a chaotic, untamed, human-free world of unbroken forests, vast swamps and deltas, plains and deserts greater than anything we might witness today is an enduring, fascinating idea, and I don't think it's a trivial one.

Fourth, and finally, dinosaurs are the subject of all kinds of questions and controversies. Sure, there are academic debates on dinosaur origins, their patterns of distribution, the shape of the dinosaur family tree and so on, but there are also areas of discussion and argument that anyone can follow: how did *T. rex* live?, what did dinosaurs look like when they were alive?, what color were they?, what noises did they make?, what was the cause of their extinction? More questions are asked about dinosaurs than any other group of animals, and

the fourth tier of my argument is that we're partly drawn to these animals because they have been, and always will be, the source of an unusual number of really interesting questions. And that's a good thing: dinosaurs are ambassadors for science, drawing people into museums and encouraging their engagement in how we study and understand the natural world.

Why, then, are dinosaurs popular? Because they look neat, because they're *awesome* in every sense of the word, because they ruled a vast, chaotic, complex wilderness, and because they're the source of a myriad of big, really interesting questions.

My vision for this book changed several times during its writing. My initial take was that I might write a guide to the changing view of dinosaurs as they've been portrayed in popular culture. Our view of ancient life is shaped very much by art, museum displays, and books. As someone who's both a dedicated collector of the literature *and* was alive during the most formative time for our modern understanding of dinosaurs (the late 1970s, the 80s and early 90s), I wanted to show how our interpretation of the dinosaurian world has its roots in the books, magazine articles, artwork, and cinematic events of those times. Sections of the book would be about the definitive authors, artists, books, and exhibits of that time period, and would discuss how our view of dinosaurs has changed in terms of how they're depicted, imagined, and described.

While some of this material has remained, I found myself gradually reducing its quantity, mostly because the better part of the book needed to be about the dinosaurs themselves. I couldn't talk about the impact

of, say, artistic portrayals of the abelisaurid theropod *Carnotaurus* without devoting text to discussions of abelisaurids and theropods, and in the end my need to give fair coverage to dinosaur groups won out.

If, however, you're going to write about dinosaur groups, one theme I find unable to shift from my mind is the fact that our views on what these groups consist of, where they belong on the tree of life, and how they relate to other groups have also changed substantially over time. In the next iteration of the book, I set about telling this story, of describing the twists and turns in our understanding of dinosaur evolution, of different concepts and models. But this simply proved intractably complex and way too technical. Such a volume does need writing and I hope one day to do it.

What we have in the end is a hopefully enjoyable but fairly deep dive into dinosaur diversity in general. My coverage isn't exhaustive (it would have to be a much longer book for that) but it's at least representative enough to give the reader a fair view of dinosaur diversity, biology, and history.

There are, however, several areas I had to mostly ignore, and for that reason we'll look at them (in brief fashion) right now. *Excluding birds* (on which, read on), dinosaurs were animals of the Mesozoic Era, a span of time that extended from 251 million years ago until 66 million years ago. The Mesozoic was preceded by the Paleozoic and superseded by the Cenozoic. The Mesozoic is divided into three subdivisions, termed periods: the Triassic (251–201 million years ago), Jurassic (201–145 million years ago), and Cretaceous (145–66 million years ago). Dinosaurs originated and

underwent evolutionary diversification during the Triassic, dominated life on land during the Jurassic and Cretaceous, and underwent extinction at the very end of the Cretaceous.

The periods are themselves generally divided into Early, Middle, and Late subdivisions (the Cretaceous lacks a "Middle" because its sediments don't warrant its recognition). The periods are also divided into shorter chunks of time called stages. These lasted, on average, around 5 million years. Dinosaur species and genera (genera = the plural of genus) tend to be unique to stages, so it's normal in technical discussions to associate a dinosaur with a stage rather than a period. *Tyrannosaurus* and *Triceratops*, for example, are animals of the Maastrichtian, the final stage of the Late Cretaceous. Stage names are unfamiliar except to specialists, so I've mostly (albeit not entirely) avoided their use in this book.

What was the world like during the 185 million years of the Mesozoic? A huge number of things changed, so it's hard to generalize. When dinosaurs originated, the continents were united in the supercontinent Pangaea. This was surrounded by a vast ocean, termed Panthalassa. Pangaea didn't represent the "ancestral state" for the world's continents: the continents had collided, separated, and collided again a few times already. During the Jurassic, Pangaea split into the northern continent Laurasia, and the southern continent Gondwana. The sea which separated the two is Tethys. The existence of these two landmasses resulted in the evolution of distinct "northern" and "southern" dinosaur faunas. Pangaea had been dominated by arid conditions

and enormous deserts, but the "post-Pangaean" world was wetter, with more extensive forests and stronger seasons.

Jurassic and Cretaceous global history was dominated by the fact that these two landmasses then gradually broke apart. Gondwana split in two as the South Atlantic began to form. India, Madagascar, Africa, South America, and Australasia all went their separate ways, some ultimately colliding with the continents of the north. Laurasia split too as North America and Eurasia broke apart, though this didn't properly happen until after the Cretaceous. These changes resulted in a more "provincial" world (one where animal groups were more likely to be restricted to a specific landmass), but also a cooler, more seasonal one. More mixing of the world's ocean currents occurred, and cooler seas developed in the north and south.

The Late Cretaceous world would have looked relatively modern in places, with plant groups and climates not that different from modern subtropical and temperate places. Climate modeling and evidence from plants and sediments show that the polar regions of the Cretaceous world were cool enough for seasonal snow and ice yet warm enough for extensive forests. Dinosaurs lived in these places, despite the winter cold and long stretches of polar darkness. On that note, it simply isn't true that the dinosaurs of the Mesozoic lived entirely in warm, humid, tropical conditions.

Where do dinosaurs fit on the tree of life? Dinosaurs are part of the great reptile group Archosauria, sometimes called the "ruling reptiles." Dinosaurs share with other archosaurs an extra cavity on each side of the

skull (termed the antorbital fenestra), a large muscle attachment site on the rear surface of the thigh, and other details. Early in their evolution, archosaurs split into two lineages. One survives today as the crocodylians, and the other as the birds. The crocodylian lineage (technically termed Crurotarsi or Pseudosuchia) includes so much more than crocodylians. An extraordinary variety of these animals thrived during the Triassic, some of which were not at all crocodylian-like and in fact looked more like prototype versions of the dinosaurs that ultimately replaced them. But this book is not about them.

The bird lineage (technically termed Ornithodira) includes a variety of small, lightly built quadrupeds and bipeds of the Triassic in addition to pterosaurs and dinosaurs. Pterosaurs were membranous-winged cousins of dinosaurs, and they don't get any detailed coverage in this book because they're not dinosaurs. The most important, most diverse, most evolutionarily successful members of the bird lineage are the dinosaurs, a group that originated around 240 million years ago during the Triassic and which survives today. Here we come to the thorny but vitally important point that birds are not just relatives of dinosaurs, but part of the group Dinosauria.

Yes, birds *are* dinosaurs, just as sauropods and stegosaurs are dinosaurs, and just as primates and bats are mammals. Specifically, birds are part of the predatory dinosaur group—properly called Theropoda—and are close kin of theropods like *Oviraptor*, *Troodon*, and *Velociraptor* (all of which were fully feathered and highly bird-like in appearance). The fossil evidence supporting this

proposal is phenomenally good, and various entries in this book discuss this evidence and how we discovered it. What's become increasingly obvious over recent decades is that birds are not "special" or "unique" relative to other dinosaurs. When birds originated during the Jurassic they were simply one of several similar small, feathery theropod groups, and it wasn't really until the Late Cretaceous—around 100 million years after their time of origin—that birds became properly unusual (by virtue of small average size, toothless horn-covered jaws, a strongly modified forelimb and pectoral skeleton, and a reduced tail skeleton). We're kidding ourselves if we ignore or downplay the fact that birds are part of the dinosaurian radiation: this is a thing that's not merely *interesting* from a nerdy point of view, it's also *important* in terms of how we imagine evolutionary history and the diversity of life. Let me emphasize that point: the fact that birds are dinosaurs is of vital importance if we want to discuss dinosaur diversity, biology, anatomy, history, or the role that dinosaurs played (and still play) in the history of life.

One result of this discovery is that dinosaurs aren't extinct, since they didn't all die out at the end of the Cretaceous. Another concerns terminology. "Dinosaur" as used in popular language most often refers to a group of big extinct reptiles. But if birds are dinosaurs—just as bats are mammals—it's technically correct to say such things as "look at the cute little dinosaurs!" when looking at parakeets or finches. To be clear, there are times when the dinosaurian nature of birds is irrelevant: areas of discussion relevant to modern birds (like birdwatching, aviculture, and conservation) can continue

without there ever needing to be any reference whatsoever to the dinosaurian nature of birds.

But there are other times when we do need to think of birds as part of Dinosauria, and when we need to make a distinction between birds and remaining dinosaur groups. The awkward but necessary term "non-bird dinosaur" is our best recourse, and you'll be seeing its use throughout this book. When "dinosaur" alone is used, it should be assumed to include, quite rightly, *all dinosaurs*: from *Triceratops* and *Diplodocus* to *Tyrannosaurus*, *Velociraptor*, *Passer*, and *Corvus*.

Also on the subject of terminology, I've assumed at least some knowledge relevant to the field when writing this book. On the names of animals, it's impossible to write about extinct animals and not use complex technical names. There's simply no way to write about scansoriopterygids or *Opisthocoelicaudia* otherwise. I remind you that the text is cross-referenced: an unfamiliar name mentioned in one entry will have its own entry elsewhere in the book.

For reasons of convenience and brevity, I use the words "taxon" (which is singular) and "taxa" (plural) a fair bit. A taxon is any biological unit at the subspecies level or above. *Brachiosaurus altithorax* is a taxon but so are *Brachiosaurus* and Brachiosauridae, Sauropoda, Dinosauria, Reptilia, and so on. I also use the similarly nonspecific term "clade" a lot. A clade is a group in which all members share the same single ancestor. Birds are a clade, sauropods are a clade, and so are dinosaurs so long as they're taken to include birds. "Non-bird dinosaurs" are *not* a clade, since some descendants of the common ancestor are excluded.

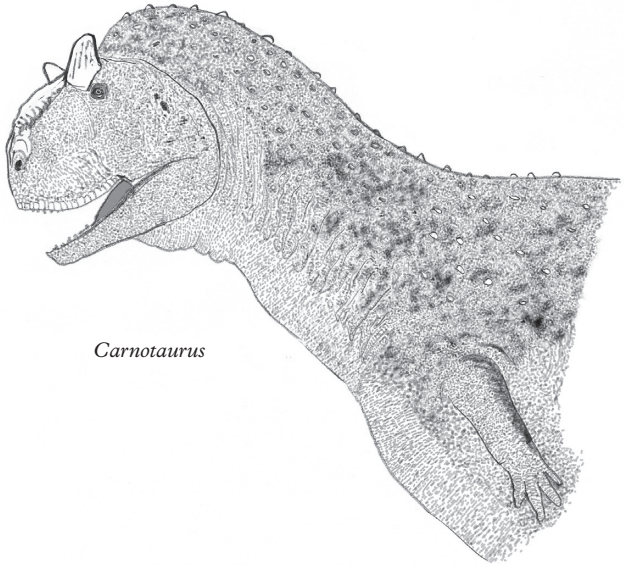
And, while on the subject of evolutionary relations . . . those of you familiar with the Linnaean system (in which genera are grouped into families, families into orders, orders into classes, and so on) might like to note that I'm one of those researchers who's given up on it. I find it misleading and damaging since it's responsible for all kinds of skewed views on evolutionary history and the diversity of life. We can avoid it altogether by referring to clades.

This being a book written for a popular audience, I've aimed to use vernacular terms for dinosaur groups where possible. Members of Thyreophora and Ornithomimidae, for example, are referred to as thyreophorans and ornithomimids, respectively. Note that vernacular terms are written with lower case first letters while their technical counterparts get a capital first letter. Alas, this becomes complicated in quite a few cases. When referring to "tyrannosaurs," for example, are we referring to members of Tyrannosauridae (the group which contains *T. rex* and its close relatives), or to members of the larger, more inclusive group Tyrannosauroidea (the group which contains Tyrannosauridae and a number of other lineages)? This sort of thing explains why the book includes terms like "tyrannosaurid" and "tyrannosauroid," but not the ambiguous "tyrannosaur."

Finally, I'm well aware that my choice of topics might seem biased and idiosyncratic. Why, for example, do John Ostrom and Halszka Osmólska get entries while many equally worthy paleontologists barely get a mention? Why are rhabdodontomorphs covered, but not elasmarians? Why have I written about the "Birds Come First" model but not the "dinosaur polyphyly"

model? Books don't have unlimited word-counts, and I had to be selective. In the end, I opted to include those things that I, personally, regard as inspirational or interesting or most relevant to the picture I wanted to paint (see those comments above about the seminal importance of the late 1970s, 80s, and early 90s). I hope you'll be forgiving and understanding, and I hope you enjoy reading the selections I've opted to include.

Dinopedia



Carnotaurus

Abelisaurids

A mostly Gondwanan, mostly Cretaceous theropod group noted for small arms, tiny hands, and broad, deep-snouted, often horned skulls. Abelisaurids became known to science during the 1980s following the description of *Abelisaurus* and *Carnotaurus*—both from the Late Cretaceous of Argentina—by José Bonaparte and Fernando Novas. Both *Abelisaurus* and *Carnotaurus* are large, with total lengths of around 8 m (26 ft). A few abelisaurids might have been larger: *Pycnonemosaurus* from Brazil perhaps exceeded 9 m (29.5 ft). *Carnotaurus* is famous for its horns and also because the only known specimen includes segments of preserved skin. These show that

conical projections (each about 4 cm [1.5 in] wide) emerged from scaly skin of typical dinosaurian sort.

Bonaparte and Novas proposed that abelisaurids were part of Carnosauria, a group used at the time as a catch-all for big, deep-skulled theropods. Within this group, they suggested that abelisaurids were especially close to the horned, Jurassic *Ceratosaurus*. But by the early 2000s, it was mostly agreed that *Ceratosaurus* and the abelisaurids were close relatives within the group Ceratosauria.

As more abelisaurids have been discovered—in Argentina, Brazil, India, Pakistan, and France—our understanding of their history has become complex. A robust clade with stocky legs—the majungasaurines—is known from Madagascar, India, and France, while the majority of South American taxa belong to the short-faced clade Brachyrostra. Abelisaurid distribution suggests that they became widespread across Gondwana prior to its breakup during the Cretaceous, in which case the rarity of African abelisaurid fossils is a sampling artifact. However, some European taxa don't fit neatly into this scenario, and their distribution might best be explained by dispersal; that is, they perhaps swam from Africa to southern Europe.

Little is known of abelisaurid biology. Their fossils are often associated with seasonally dry, wooded environments, and their powerful skulls, well-muscled necks, and serrated, bladelike teeth show that they were predators. A gnarly texture on the side of the skull suggests that some species had a thick, hornlike facial covering, so it might be that these species stunned or injured prey with an impact from the face. *Carnotaurus*

has enormous neck vertebrae and must have had a thick, bulldog-like neck, so it presumably subdued prey—perhaps ornithopods and juvenile sauropods—with a crushing bite.

Carnotaurus has proved an irresistible subject for artists and has also become a staple of popular books on prehistoric life, the consequence being that it's featured in films like Disney's *Dinosaur* of 2000 and the second *Jurassic World* movie.

See also Ceratosaurs.

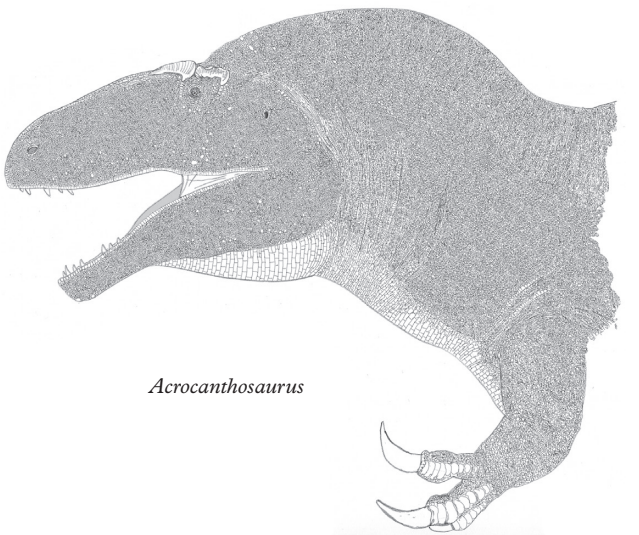
Allosauroids

One of several theropod clades that evolved large size and an ability to kill giant prey. Allosauroids are associated mostly with the Late Jurassic and Early Cretaceous but persisted to the end of the Cretaceous in South America. Their oldest fossils date to the Middle Jurassic, but it's likely that they—together with megalosauroids and coelurosaurs—are part of an evolutionary radiation that happened around 180 million years ago, during the Early Jurassic.

Allosauroids are mostly (there are exceptions) between 6 and 10 m long. This, combined with their deep, narrow skulls, serrated teeth, and powerful forelimbs (equipped with claws that recall eagle talons), indicates that they predated on ornithopods, stegosaurs, and small sauropods, and such is confirmed by bite marks preserved on bones. Evidence of predation on other theropods, including cannibalism, is also documented by fossils.

Allosauroidea is named for *Allosaurus*, an iconic theropod associated with the Morrison Formation but

also known from Portugal. *Allosaurus* and its close relative *Saurophaganax* (also of the Morrison Formation) form the allosauroid clade Allosauridae, one of three main allosauroid clades. The second includes mid-sized, *Allosaurus*-like animals in addition to much larger theropods associated mostly with Africa and South America. This is Carcharodontosauria, a clade significant enough that it gets its own section in the book. The third main allosauroid clade is Metriacanthosauridae (known for a while as Sinraptoridae). Metriacanthosaurids have short facial bones compared with other allosauroids, tall bony spines on their vertebrae, and short hands. They're anatomically archaic compared with other allosauroids.



Acrocanthosaurus

Allosaurus used to be depicted as a nondescript big theropod, similar to *Megalosaurus* and likely descended from it. Today we have a more sophisticated view of its appearance. It had triangular horns in front of its eyes and paired crests along the top of the snout. The fact that some *Allosaurus* specimens are shorter-faced than others was always a cause of confusion, sometimes taken to mean that *Allosaurus* included two different taxa, the longer-snouted of which should be called *Creosaurus*. Modern work has shown that this short-faced look was due to the incorrect assembly of a particular skull, and the short-faced *Allosaurus* depicted in so many books and articles of the past never existed.

When it comes to behavior and lifestyle, we're confident that allosauroids of all sorts were predatory. It seems likely that they used their formidable hand claws to grab prey and restrain or injure it. Indeed, a 2006 study of the carcharodontosaurian *Acrocanthosaurus* found that its fingers could withstand substantial bending and flexing consistent with such behavior.

The skull was the primary weapon, though, and the proportions of the head, neck, and arms mean that the mouth would always make contact with a prey item before the hands did. The fact that the skull is deep and narrow suggests that it was good at resisting vertical forces, and a popular idea on these dinosaurs is that they took rapid, slicing bites from prey, the aim being to cause blood loss and shock rather than debilitating, crushing bites. In 2001, Emily Rayfield and colleagues used finite element analysis (or FEA) to test how a digitally modeled *Allosaurus* skull withstood compression and deformation. They found that *Allosaurus* had

a weak bite but was able to tolerate a huge amount of stress, all of which is consistent with use of the upper jaw as a hatchet-like weapon effective on large prey. That 2001 Rayfield-led study was pioneering, and FEA has since been applied widely to dinosaur skulls, and to those of other animals (living and fossil) too.

See also Carcharodontosaurs; Megalosauroids.

All Yesterdays

A 2014 book devoted to the artistic portrayal of Mesozoic dinosaurs and other extinct animals, described by some as the most significant paleoart-themed work of modern times. I'm biased, since I'm one of the authors (the others are John Conway and C. M. "Memo" Kösemen, both of whom created the book's color artwork). *All Yesterdays* serves two main functions. The first is to point out that prehistoric animals may have engaged in all kinds of unexpected, surprising, and extreme pieces of behavior, and that artists might consider depicting these rather than the tropey scenes featured on more regular occasion. The second is to draw attention to embedded conventions in paleoart, in particular the tendency to show dinosaurs as "shrink-wrapped"; that is, with the absolute minimum of skin, fat, and muscle. We mostly had in mind the svelte, skeletal dinosaurs of Greg Paul and those who've followed him, though our call for change is not in any way meant to be disrespectful. Indeed, we count Greg as among our most formative of influences.

All Yesterdays emphatically does not promote an "anything goes" approach when it comes to paleoartistic speculation, since we made it clear that existing data

(on anatomy, ecology, and behavior) must be taken into account before any layers of speculation are added on. Nevertheless, the book has encouraged artists and illustrators to consider a more diverse range of possibilities of life appearance and behavior than convention would permit. This has been termed the *All Yesterdays Movement* and many modern paleoartists can be considered part of it. Not everyone likes what we've said, and we do of course have our haters and detractors; *c'est la vie*.

See also Greg Paul.

Alvarezsaurs

A clade of mostly small, long-legged, short-armed maniraptorans, associated mostly with the Late Cretaceous of South America and eastern Asia.

The alvarezsaur story starts with the 1991 naming of *Alvarezsaurus* from the Late Cretaceous of Argentina, a meter-long, long-tailed theropod of uncertain affinities. José Bonaparte, its describer, thought it perhaps similar to ornithomimosaurs but unique enough for its own group, which he termed Alvarezsauridae. Meanwhile, a team working on Late Cretaceous fossils from Mongolia's Gobi Desert, and led by famed Mongolian paleontologist Altangerel Perle, discovered a similar, small, lightly built coelurosaur notable for its highly muscular, picklike, one-clawed forelimbs. They named it *Mononykus* (meaning "one claw") in 1993, and suggested that it was an unusual, flightless bird, more closely related to modern birds than *Archaeopteryx*.

The bizarre anatomy of *Mononykus* led to a great deal of discussion about its lifestyle, most experts agreeing that its forelimbs were specialized for the breaking

apart of wood or soil in quest of ants and termites. In modern animals, similar picklike forelimbs are seen in pangolins and anteaters. These animals don't just have picklike forelimbs; specializations in the skull and chest are also linked to their diet and way of life. The more we've discovered about alvarezsaurs, the more their anatomy has appeared consistent with this lifestyle. Their skulls were lightly built, their jaws slender, their teeth tiny, they might have had a protrusible tongue, and their chest bones and spine look adapted for withstanding the forces involved in picklike use of the forelimbs. The overall shape of these dinosaurs shows that they can't have been diggers, burrowers, or climbers; instead, they were most likely good at breaking apart insect nests located in soil mounds or rotting wood. Their long, slender legs show that they were able to cover ground at speed, which makes sense given that ant and termite nests are sometimes well separated in the landscape.

It was eventually discovered that *Mononykus* wasn't *really* one-clawed (it actually retained small, clawed second and third fingers on its hands as well) but some other alvarezsaurs were, like *Linhenykus* from China. Numerous additional alvarezsaur taxa have been named since, including *Patagonykus* from Argentina, *Albertonykus* from Canada, and *Parvicursor*, *Shuvuuia*, and *Albinykus* from Mongolia. By the late 1990s, it was obvious that *Alvarezsaurus* from Argentina was also a member of this clade, which means that the name originally chosen by Bonaparte—Alvarezsauridae—should be applied to the whole group. And new discoveries and additional studies show that this clade isn't part of

Mononykus

Avialae (the bird clade), but instead located elsewhere within Maniraptora, perhaps close to the group's origin.

One issue remains. *Mononykus* and the other taxa mentioned so far are highly specialized, and quite different from other maniraptorans. What were ancestral, older members of the group like? A few Late Jurassic, Chinese maniraptorans appear to provide the answer. These animals—they include *Haplocheirus* and *Shishugounykus*—are alvarezsaurid-like in some details but larger (around 2 m [6.5 ft] long), possess large,

grabbing hands with three prominent fingers, and overall appear far more like conventional maniraptorans. These taxa are excluded from the clade Alvarezsauridae but are included with them in the more inclusive Alvarezsauroidea.

See also Maniraptorans.

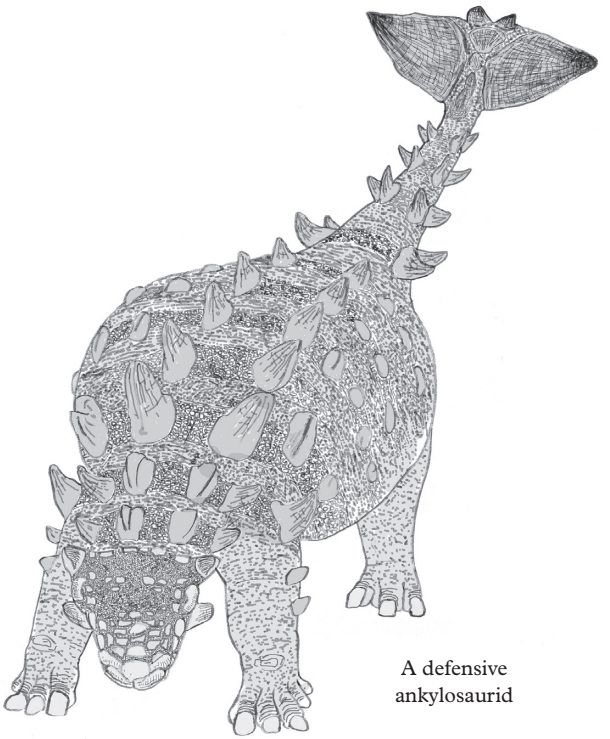
Ankylosaurs

The great armored ornithischians of the Jurassic and Cretaceous, famous for their spikes, plates, and tail clubs and often described as "dinosaurian tanks." All ankylosaurs were quadrupeds, and their ancestral condition—which we can infer from thyreophorans like *Scelidosaurus*—was to have parallel rows of horn-covered bones (termed osteoderms) arranged along the top and sides of the neck, back, and tail. In some ankylosaurs, osteoderms on the shoulders, chest, hips, and tail formed spikes or curved blades. In others, osteoderms on the neck's upper surface and sides were fused into "half-rings," while osteoderms at the tail tip were combined to form a club. Thorn- and pebble-like osteoderms were located on the limbs, bodies, and tails of some species.

Additional ankylosaur features include a modified hip girdle where the socket is closed (or partly closed), fusion of various sections of the vertebral column, and a deep shoulder blade with enlarged muscle attachment sites. Dinosaurs tend to be tall-bodied, long-legged creatures with aesthetically pleasing lines and streamlined, muscular bodies. I can't help but think of ankylosaurs as utterly detached from this: as low-slung, stumpy-legged, jagged, comically broad animals

that lived close to the ground. They are—I submit—the most atypical dinosaurs, the ones whose evolution was the least "predictable" given dinosaurian beginnings.

Some ankylosaurs have a slender snout, others a short, broad one. Large, complicated nostrils and long, looping nasal passages are present in some and might have been used in temperature control and perhaps noise making. It's common for there to be a pavement



A defensive ankylosaurid

of bony plates across the top of the ankylosaurian skull. Horns project from the back of the skull in some short-snouted forms and armor plates cover the cheek region, side of the lower jaw, and even the eye socket in some species (these eye plates were mobile and embedded within the eyelids). The smallest ankylosaurs were around 1 m (3 ft) long as adults while the biggest reached 9 m (29.5 ft) and perhaps 8 tonnes (8.8 tons).

Our view on how ankylosaur taxa might be arranged was vague prior to the late 1970s. At that time, Walter Coombs argued that ankylosaurs could be divided into the two clades Nodosauridae and Ankylosauridae. Nodosaurids include the longer-snouted taxa and those with neck and shoulder spikes. Ankylosaurids, meanwhile, include both long-snouted and short-snouted taxa, and those with tail clubs.

Several Jurassic and Early Cretaceous ankylosaurs from Europe, Asia, and North America share a bony shield covering the upper surfaces of the hips, and shoulder spines that have grooves along their rear margins. Coombs included these taxa within Nodosauridae, but a view which has become more popular since 2001 is that they deserve to be recognized as a third clade, termed Polacanthidae. Experts disagree on whether Polacanthidae is a clade and where its constituent taxa belong.

The massive, wide bodies of ankylosaurs and small, vaguely leaf-shaped teeth (which resemble those of herbivorous lizards) show that they were herbivores, most likely specializing on leaves. Work on ankylosaur jaws and tooth wear shows that at least some had complex chewing cycles in which the two halves of the lower jaw

rotated around their long axes as the jaw was closed. At the same time, the whole jaw underwent a palinal movement, meaning that it was pulled backward.

Stomach contents from the Australian *Kunbarrasaurus* indicate a diet of fruits, twigs, and leaves; those of the Canadian *Borealopelta* reveal that it ate mostly ferns. Gastroliths in *Borealopelta* confirm their presence in at least some ankylosaurs. An intriguing but unverified suggestion is that some ankylosaurs were omnivorous, perhaps even insectivorous. After all, they superficially recall gigantic armadillos, and the arms and snouts of some taxa look suited for digging or rooting. A big surprise was revealed in 2016 by *Liaoningosaurus* from Liaoning Province in China. It has fish preserved as stomach contents and a few of its traits (small size, spiky tooth cusps, and reduced armor) suggest amphibious habits. If this interpretation of *Liaoningosaurus* is accurate, it shows that ankylosaurs were more diverse in ecology and diet than previously thought.

Outside of diet, we have but a few glimpses of ankylosaur behavior and biology. In a few cases, individuals have been discovered together, so perhaps some lived in groups. Ankylosaur armor has usually been imagined as serving a defensive role, and the shoulder spikes of some taxa and tail clubs of others were surely good at keeping theropods at bay and even at wounding them fatally. In a series of experiments, ankylosaur expert Victoria Arbour calculated the whacking power of a big ankylosaurid's tail club and showed that it was powerful enough, and sufficiently mobile, to break bones. Weapons in animals typically serve in mating battles and sexual displays, their anti-predator roles being

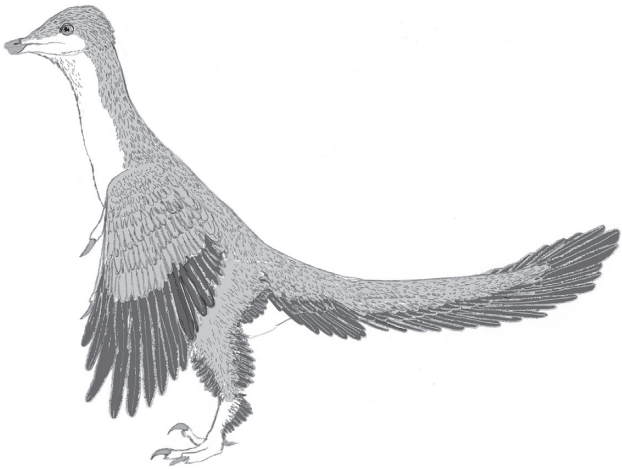
ancillary. Did ankylosaur armor similarly evolve within this context? We don't know, but if this were so, females and males may have been equally belligerent given that members of both sexes were (so far as we know) similarly armored. All round, ankylosaurs must have been incredible in appearance and formidable in habits.

See also Ornithischians; Thyreophorans.

Archaeopteryx

The fabled "first bird" or "Urvogel" of the Late Jurassic, discovered in the Solnhofen Limestone of Bavaria, Germany. *Archaeopteryx* is a crow-sized maniraptoran, currently known from 12 specimens. Several preserve feather impressions. The timing of *Archaeopteryx*'s discovery couldn't have been better, as it happened just after Darwin published *On the Origin of Species* in 1859. Here was evidence that forms of life "intermediate" between the groups of today existed in the past. *Archaeopteryx* was a bird, but a bird with "reptilian" traits, like teeth and a long bony tail.

Between the 1860s and 1970s, views on what *Archaeopteryx* was like were vague. It was imagined as a generalized tree dweller, something like a toothed magpie or cuckoo, that perched and flew clumsily. Perhaps it was more of a glider than a flapper. The Dinosaur Renaissance led to a recasting of *Archaeopteryx*. It had obvious similarities with theropods like *Deinonychus*, and—so John Ostrom argued—might be better regarded as a small, feathered theropod that hunted on the ground. Ostrom even suggested that *Archaeopteryx* used its wings to help capture insects. During the 1980s, this view was taken further by Greg Paul, who argued



that *Archaeopteryx*, while flight-capable, lived on arid islands where trees were absent and prey must have been gleaned from the water's edge. Paul also argued that *Archaeopteryx* should be regarded as a miniature member of the clade otherwise known for including *Deinonychus* and its kin, the Dromaeosauridae.

The size and shape of its teeth suggest that *Archaeopteryx* ate arthropods and small vertebrates, perhaps including fishes. We might speculate that it sometimes preyed on larger animals, perhaps the baby pterosaurs which were abundant in its environment. Exactly how proficient *Archaeopteryx* was as a flier has been the cause of dispute. Views vary between those who interpret it as proficient and able to launch from the ground, and those who suggest it was flightless. It should also be added that there are no reasons to think

of *Archaeopteryx* as adapted for perching; not only did it live in a habitat where trees were rare or absent, its foot anatomy looks suited for life on the ground.

The history of how we should use the name *Archaeopteryx* and how many taxa there might be is complicated. An isolated Solnhofen feather, reported in 1861, was regarded for a time as the key specimen to which the name *Archaeopteryx* was attached; that is, as the holotype. This was always a dangerous position because it was difficult if not impossible to demonstrate that the feather belonged to the same taxon as the skeletons. Current thinking is that it probably *is* from *Archaeopteryx*, but this has been disputed in the past. The so-called London specimen of *Archaeopteryx*—discovered in 1861—is now regarded as the holotype, but debate has surrounded how many taxa are represented by the 12 known specimens. Are they all growth stages and size variants of the one species *A. lithographica*, are there two, three or more species of *Archaeopteryx*, or are the differences between the specimens sufficient to recognize more than one genus? (*Archaeornis*, *Jurapteryx*, and *Wellnhoferia* are all on the roster of suggested names). The majority view at the time of writing is that there's a single genus and that it contains *A. lithographica*, *A. siemensii*, and *A. albersdoerferi*. One fossil long misidentified as a specimen of *Archaeopteryx* is today known to be a German member of the (mostly Chinese) maniraptoran group Anchiornithidae, and this is *Ostromia*, named in 2017 for the so-called Haarlem *Archaeopteryx*. Its name commemorates John Ostrom.

Today, *Archaeopteryx* is only one among several archaic, Jurassic avialans, some of which (several Chinese

anchiornithids and scansoriopterygids) are older than it is. It remains generally agreed that *Archaeopteryx* is part of Avialae, the bird clade, and that it's closer to modern birds than are anchiornithids. However, a few studies have found *Archaeopteryx* to be located elsewhere in the family tree, most frequently close to Dromaeosauridae.

See also Birds; John Ostrom; Maniraptorans.

Bakker, Robert (or Bob)

American paleontologist who spearheaded the Dinosaur Renaissance. Through technical papers, magazine articles, compelling artwork and a popular book—*The Dinosaur Heresies*, published in 1986—Bakker promoted the view that dinosaurs were one of evolution's greatest success stories, and were behaviorally complex, highly active, biomechanically sophisticated, hot-blooded animals. Bakker began his academic career with a bachelor's degree from Yale University, completed under John Ostrom. In 1971, he was awarded a PhD at Harvard, and his illustration of a sprinting *Deinonychus*, poised mid-stride (albeit without feathers), accompanied Ostrom's seminal 1969 description of this dinosaur.

From 1968 onward, Bakker published papers which brought dinosaur energetics, ecology, and evolutionary success to wide attention, and if there's one thing he's known for it's for arguing that non-bird dinosaurs were endotherms (that is, that they were "warm-blooded"). This work inspired responses and counterarguments from colleagues who disagreed with Bakker's interpretations of the data. Bakker's 1971 article on sauropods was integral to a paradigm shift that moved these

dinosaurs away from wetlands and toward parklands and plains. A 1974 article coauthored with Peter Galton made the case for the idea that dinosaurs were a clade rather than a set of archosaur lineages that descended from distantly related ancestors. And Bakker's 1975 *Scientific American* article—titled "Dinosaur Renaissance"—marked mainstream awareness of these ideas and their impact.

Despite all this, some paleontologists would have it that Bakker's contributions to science aren't notable and that emphasis of his role (like that occurring here) reads like hero worship. A fairer appraisal is that his work made dinosaur science more visible by inciting controversy and argument, and that this both attracted researchers and encouraged more rigorous efforts to examine the relevant questions. In 1994, photojournalist Louie Psihoyos made the memorable statement that "trying to imagine modern dinosaur paleontology without Bob Bakker is like trying to imagine the sixties without rock and roll," which I think is a pretty accurate statement.

Bakker has, of course, published many studies beyond those of the 1960s and 70s, but it has to be said that some of this work has a more *esoteric* air. The studies include those positing a stegosaurian identity for nodosaurids (1988), a whale-like ecology for carcharodontosaurids and *Spinosaurus* (1992), a sabretooth-cat-like ecology for *Allosaurus* (2000), and an amphibious lifestyle for *Ceratosaurus* (2004). Bakker was lead author on the 1988 study advocating the distinct nature of *Nanotyrannus* and promoted use of the name *Brontosaurus* prior to its official resurrection. He published a

novel in 1995, titled *Raptor Red*, which tells the life story of a *Utahraptor* from the point of view of the animal.

Over the course of his career, Bakker has been affiliated with various museums and institutions. An attachment to the education of children and the public is evident and he still performs public lectures and writes books for kids. A biographical detail sometimes touched on in interviews and articles is that Bakker comes from an evangelical Christian background and is a qualified minister. He promotes the view that religion and science are in no way incompatible and that the story of creation given in the Bible is not meant to be taken literally.

See also *Brontosaurus*; Dinosaur Renaissance; John Ostrom; *Nanotyrannus*.

Birds

A diverse animal group (containing more than 10,000 living species) that occurs worldwide and is famous for the feathers, toothless beaked jaws, and flight ability of the majority of its species. Birds are maniraptoran coelurosaurs closely related to dromaeosaurids and troodontids. This means that dinosaurs did not become extinct at the end of the Cretaceous *and* that dinosaurs have been substantially successful throughout the so-called Age of Mammals.

All living birds belong to a huge clade called Neornithes. The neornithine body is superbly adapted for flight. The skeleton is pneumatized, a keel on the sternum anchors large muscles which power the wings; the enormous feathers of the forelimbs and tail form flight surfaces the animal can tightly control; the eyes

and brain are unusually large; and the feet (typically equipped with an enlarged inner toe that fully opposes the other three) are specialized for perching. The average size for a neornithine is around 30 g (1 oz).

The technical name long preferred for the bird clade is Aves. An alternative argument is that "Aves" is best restricted to neornithines (since these alone have the combination of features typically regarded as special to birds), and that the whole of the clade is best termed Avialae. Unfortunately, experts disagree on this, meaning that Aves and Avialae are *both* currently in use for the clade that includes *Archaeopteryx*, neornithines, and all lineages in between.

It's been agreed since the 1800s that birds are "glorified reptiles." More specifically, it's obvious that birds are archosaurs, since they share anatomical and behavioral features with crocodylians. An even more specific view—that birds might be dinosaurs—was mooted during the 1860s when famed "Darwin's bulldog" Thomas Huxley noted the birdlike hips and legs of the coelurosaur *Compsognathus* and the ornithischian *Hypsilophodon*. Consequently, the idea that birds are allied to dinosaurs became popular during the late 1800s and early 1900s. Experts of this time tended to have vague views on how animal groups were related, so the idea of a bird-dinosaur affinity was consistent with the possibility that birds might also be close to early archosaurs or even pterosaurs.

By the 1920s, the consensus was that birds had evolved from a group of archosaurs termed "pseudosuchian thecodonts" that were themselves ancestral to dinosaurs and other archosaur lineages too. One study

Erithacus,
a modern bird

in particular—Gerhard Heilmann's 1926 book *The Origin of Birds*—did much to establish this view as the one best supported by evidence. An ironic aspect of the book's success is that Heilmann was an amateur scientist and artist, ridiculed and ignored by scientists in his native Denmark, but mostly unknown elsewhere and thus assumed to be authoritative. Anyway, the "pseudosuchian" view became textbook wisdom for the next few decades.

It was eventually overturned in the late 1960s following John Ostrom's work on *Deinonychus*. Today, Ostrom's conclusions are fantastically well supported by tens of Jurassic and Cretaceous fossils. These include birdlike non-birds in addition to a vast number of early

birds, many of which possess anatomical traits that are "intermediate" in shape and proportion between those of dromaeosaurids and those of neornithines.

Prior to the 1980s, the early bird record consisted of *Archaeopteryx*, the toothed Cretaceous seabirds *Ichthyornis* and *Hesperornis*, and little else. Today we know of several bird clades which are archaic relative to neornithines (many have teeth and clawed fingers), but closer to them than is *Archaeopteryx*. The most important of these are the enantiornithines (sometimes called "opposite birds"), a large, diverse radiation of archaic birds that include taxa recalling seabirds, waders, hawks, and finches.

The most archaic fossil birds show that birds were initially just one of numerous maniraptoran clades, all of which looked similar during the earliest stages of their history, and all of which started their history as small generalist predators or omnivores. Only later did birds evolve the peculiarities associated with neornithines, and in fact the most profound transition in bird evolution is the one that separates neornithines from their nearest relatives. This event occurred during the Cretaceous, and we know this because early members of the main neornithine clades—like those leading to ducks and gallinaceous birds—are known as Late Cretaceous fossils.

Working out how the numerous neornithine clades are related has been a formidable task; a vast literature exists on this topic, and numerous ideas have been put forward. A consensus has emerged since 2006 thanks to several major genetic studies. These agree in showing that ratites and tinamous (palaeognaths) form

the sister-group to remaining neornithines, that anseriforms (ducks and kin) and galliforms (gallinaceous birds) are united within Galloanserae, and that remaining neornithines diverged in the following order: swifts, nightjars and kin (Strisores), bustards, pigeons and kin (Columbaves), cranes, rails and kin (Gruiformes), waterbirds, seabirds and kin (Aequorlitornithes), raptors (Accipitriformes), owls (Strigiformes), woodpeckers, rollers and kin (Coraciimorphae), and parrots, falcons, songbirds, and kin (Australaves). Songbirds—properly, Passeriformes—are the largest single bird clade, containing more than 60% of living bird species.

A significant percentage of bird species are endangered by human activity, and it looks likely that entire clades will be lost within coming decades. This book is about extinct animals, not those alive today, but as a conscientious person interested in the natural world, do remember to do what you can to ensure that birds and other animals persist into the future.

See also *Archaeopteryx*; Birds Are Not Dinosaurs; John Ostrom; Maniraptorans.

Birds Are Not Dinosaurs (or BAND)

The intellectual movement, led by a group of ornithologists and paleontologists, which contests or dismisses evidence showing that birds are theropods. In its earliest stages, the "birds are not dinosaurs" movement (BAND from hereon) wasn't a movement at all, but merely the opinion of a number of authors who were unconvinced by Ostrom's proposal that birds are close kin of *Deinonychus*-like maniraptorans. Which is fine,

because skepticism is part of science, and all claims deserve to be checked and tested. What *isn't* fine is the cherry-picking and misinterpretation of data that continues even after it's been shown to be inaccurate or misplaced, and attempts to dismiss data because it conflicts with a preferred scenario.

Things kicked off with papers by Max Hecht, Samuel Tarsitano, and Larry Martin, all of whom argued (between 1976 and the early 2000s) that the features used by Ostrom to link birds with theropods were not as robust as he'd thought. They argued that bird and theropod wrists and ankles were formed from different bones and that the bird hand is formed of different digits from the dinosaurian one. The obvious problem with these criticisms is that the relevant data on birds come from embryology, an area where data on Mesozoic animals are somewhat deficient. Also problematic is that the "non-theropod" conditions supposedly present in the wrists and ankles of embryonic birds are very much open to interpretation, a fact never made clear by the authors concerned.

In 1980, ornithologist Alan Feduccia also contested the view that birds are theropods, initially in his book *The Age of Birds*. His primary argument was that birds and feathers surely evolved among tree-dwelling animals, that theropods can thus be excluded from avian ancestry, and that a group of small archosaurs termed "pseudosuchians" were the real bird ancestors. Feduccia expanded his argument in his 1996 book *The Origin and Evolution of Birds*, in technical papers, and in his 2012 *Riddle of the Feathered Dragons*. He's been the primary go-to person on the BAND argument throughout

the 1990s and twenty-first century and is almost synonymous with the idea today.

How have these researchers dealt with the discovery of feathered oviraptorosaurs, dromaeosaurids, and so on? They've been hugely inconsistent is how. Martin and Feduccia initially argued that dromaeosaurids and kin were not birdlike at all, the perceived similarities being due to convergent evolution, they said. When the feathered oviraptorosaurs *Caudipteryx* and *Protarchaeopteryx* were announced in 1998, Feduccia declared that they must be flightless birds, "Mesozoic kiwis," he said. When feathered dromaeosaurids (like *Sinornithosaurus* and *Microraptor*) were reported in the early 2000s, Feduccia declared them birds too (thereby denouncing years of arguing that they couldn't be anything to do with birds), though some of his papers state on some of their pages that animals like *Microraptor* didn't have feathers at all. Indeed, a fundamental issue with the BAND contention is that they decry any indication of feathers in dinosaurs, but immediately declare any dinosaur discovered with feathers to be a bird.

As for those theropods with more filament-like feathers, Feduccia and colleagues have argued that the filaments are artifacts of some sort, the favored claim being that they're misidentified internal skin fibers. This is despite the fact that they're external to the skin, look nothing like internal skin fibers, and contain pigments that are only ever present on the outside of an animal.

These authors have also argued that *Archaeopteryx* has been misunderstood, and that it was less theropod-like than Ostrom thought. This claim has been a mainstay BAND argument; they've interpreted

Archaeopteryx as possessing sprawling hind limbs, back-turned pelvic bones, and an opposable inner toe, features which would make it different from maniraptorans like dromaeosaurids. Martin also argued that the teeth of *Archaeopteryx* and other toothed birds are unlike those of theropods. None of these claims are correct. All have been refuted by detailed work on *Archaeopteryx* and other taxa.

Views differ on how to receive those promoting BAND—sometimes called the BANDits. A common view in science is that criticism and skepticism should be encouraged since they promote checking and testing and thereby cause theories to become more robust. The BANDits could therefore be the good guys whose decades of criticism caused others to up their game, and whose tactics should be celebrated and appreciated. Denouncing them as a tiresome group of nay-sayers (and labeling them with an acronym) could be considered divisive and rude.

An alternative view is that the actions of the BANDits have been erosive and destructive, that they've caused many scientists to waste time responding to their claims, that they've behaved more like politicians than scientists (at one point even wearing badges with "Birds Are Not Dinosaurs" as a slogan), and that their continual gaslighting and sniping has done little more than make evolutionary science look weaker, in terms of intellectual structure and factual basis, than it is. Indeed, if there's one evolutionary biologist who creationists love to quote, it's Alan Feduccia. For these reasons, some experts—ornithologist Richard Prum is one of the best examples—argue that BANDit arguments should be

ignored entirely, and that what they're doing isn't science, and hasn't been science for decades.

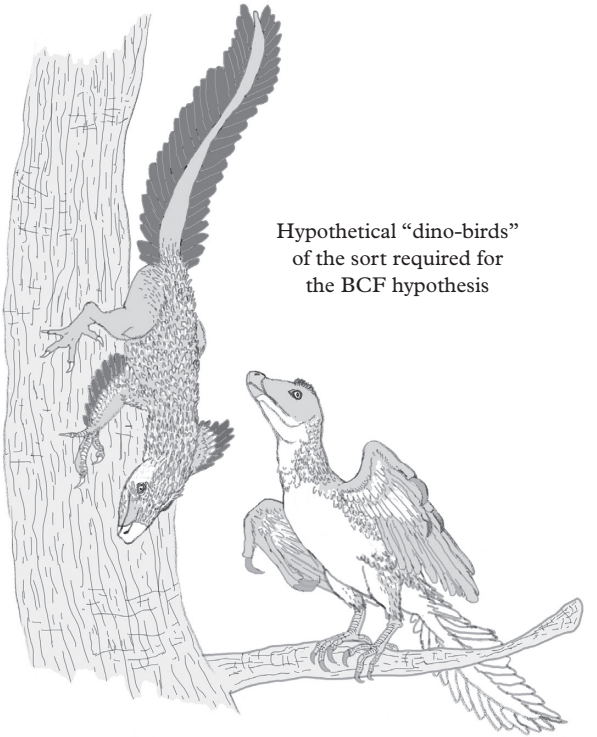
See also *Archaeopteryx*; Birds; Maniraptorans; John Ostrom.

Birds Come First

A non-standard hypothesis which posits that all dinosaurs descended from small, mostly quadrupedal, tree-climbing "dino-birds" that were the direct ancestors of birds. According to this model, dubbed "Birds Come First" (BCF hereafter), "dino-birds" form a central dinosaurian lineage and every clade that evolved from them—excepting birds—was an evolutionary dead-end where large size and terrestrial habits evolved in parallel.

BCF is the intellectual brainchild of George Olshevsky, a writer and researcher prominent in the dinosaur fandom community of the 1980s and 90s. Olshevsky's fame was due mostly to his *Archosaurian Articulations* newsletter of the late 80s, his maintenance and publication of a taxonomically thorough list of Mesozoic archosaurs, and his communications to the dinosaur mailing list (or DML), an internet chatroom that—prior to the rise of blogging, Facebook, and Twitter—was the main port of call for hot news and discussion on matters Mesozoic. BCF was never published in a formal venue, but via magazine articles, most notably those in *Omni* in 1994 and Japan's *Dino Press* in 2001.

Olshevsky's idea was in part inspired by the fact that birdlike details of anatomy have been pushed ever further "down" the archosaur family tree. He also regarded some details of dinosaur anatomy (like the shortened inner toe typical of bipedal ornithischians



Hypothetical "dino-birds" of the sort required for the BCF hypothesis

and theropods and the winglike forelimbs of maniraptorans) as making no sense within the conventional narrative. Greg Paul's model of secondary flightlessness in non-bird coelurosaurs was also credited as an inspiration, since all Olshevsky did, essentially, was to expand Greg's model to the whole of Dinosauria.

There was a time during the 1990s when BCF was considered a plausible model of dinosaur evolution. Or,

at least, it was in the student community of which I was part. However, the dino-birds integral to the model have never been found. Well, caveat: BCF contends that several unusual reptiles of the Triassic—like the drepanosaurs and the amazing plumed *Longisquama*—are dino-birds, but this view is not shared by the scientists who've studied these fossils. Furthermore, the distribution of anatomical features in early members of the relevant clades do not match BCF's predictions. According to BCF, early ornithischians, sauropodomorphs, and theropods should have climbing specializations, as should other animals close to the root of the dinosaur tree. But they don't have *any* features linked to a climbing lifestyle. The idea utterly failed to win support from any publishing academic, Olshevsky no longer publishes and is not active on social media, and the model is mostly unknown except to dino-nerds of the nerdiest caliber.

See also Birds; Greg Paul; Maniraptorans.

Bone Wars

The unofficial name for the nineteenth-century dispute between the American paleontologists Edward Drinker Cope and Othniel Charles Marsh between the early 1870s and 1890s. The Bone Wars overlap with (but are not entirely the same as) the Great Dinosaur Rush, the period during which the US western interior was plundered for its dinosaurs. The discoveries made during this time—*Stegosaurus*, *Allosaurus*, *Apatosaurus*, *Triceratops*, *Brontosaurus*, and so on—were foundational to the science of vertebrate paleontology, to the public's fascination with dinosaurs, and to the

establishment and reputation of the great museums of the East.

Cope and Marsh were both ambitious, independent men with strong financial backing. Cope in particular was extraordinarily accomplished, his work involving living fishes, amphibians, and reptiles in addition to fossils. The two were initially on good terms and, during the 1860s, even named species after each other. But their relationship soured as they clashed over who'd secured the rights to fossils from certain areas, and as they disagreed over the names and identities of specific fossils. They raced to name species before the other did, and each deliberately chose not to credit the work of the other.

It's usually said that the reason for their falling out was an event of 1870 in which Marsh pointed out that Cope had reconstructed the plesiosaur *Elasmosaurus* with the skull on the end of its tail. Cope aimed to buy and replace all copies of the work which included this faulty reconstruction, and Marsh enjoyed telling this story as an example of Cope's fallibility and vanity. While it's likely that this event did contribute to their bad relations, it was pioneering paleontologist Joseph Leidy who initially corrected Cope on this detail, not Marsh. And Marsh didn't start telling this story until 1890, long after he and Cope had fallen out. A case can be made that the conflict between Cope and Marsh arose as a slower, more incremental event involving numerous small disagreements.

Regardless, the two were enemies by 1873 and sought to outdo the efforts of the other for the rest of their careers. Both sent prospectors and fossil finders

into the field to obtain fossils before the other. There was spying and even the attempted theft of discoveries. Events came to a head in 1890 with a public battle strewn across the pages of newspapers. There were allegations of corruption, misuse of government funds, and a resulting investigation by congress.

Much has been written on the legacy of both men. Both made major contributions to paleontology, and their names are entwined with any discussion of North American dinosaurs, especially of the Morrison Formation. But their antics harmed the reputation of American paleontology, their rushed means of collecting and reconstructing fossils resulted in the loss of information and avoidable anatomical mistakes, and their race to slap names on new species resulted in a confused picture for those who studied fossils in the years that followed. Cope was also an appalling racist and sexist, and quite happy to express these views in print. Cope died in 1897, Marsh in 1899.

Some authors have described the Bone Wars as part of a grand Heroic Period in the history of dinosaur research. Cope and Marsh probably saw themselves as heroes, but I don't think the rest of us should.

See also *Brontosaurus*; Morrison Formation.

Brachiosaurids

Few sauropod clades can be considered familiar outside the dinosaur research community. Among the few are the brachiosaurids, a Late Jurassic and Early Cretaceous macronarian clade famed for great size and interesting proportions. Brachiosaurid forelimbs are as long as or longer than the hind limbs, the shoulders are

taller than the hips, and the tail is proportionally short. An arching bony crest is present over the forehead and snout, though not in all taxa. Most experts agree that the neck was held near-vertically, the result being great vertical reach. Presumably, brachiosaurids fed from tree crowns where they used their wide, rounded jaws and robust, spatulate teeth to bite off leaves and small branches. Brachiosaurids were typically the biggest dinosaurs in their faunas, in cases reaching 22 m (72 ft) and exceeding 40 tonnes (44 tons). They weren't all giants, though. *Europasaurus* from the Late Jurassic of Germany was an island dwarf just 6 m (19.5 ft) long and less than a tonne (approximately 1 ton) in weight.

The exemplar of the group—*Brachiosaurus altithorax*—was discovered in the Morrison Formation of Colorado in 1903, and the significance of its unusual proportions wasn't lost on its describer, Elmer Riggs; the name means "arm lizard with deep chest." What was believed to be a second species—*B. brancai*—was described from Tendaguru in what's now Tanzania in 1914 but is now recognized as the separate genus *Giraffatitan*.

A portrait of *Giraffatitan*

In the years following the description of these taxa, fossils from the USA,

western Europe, eastern Asia, Australia, and elsewhere were identified as additional brachiosaurids. These include teeth, vertebrae, and skull fragments dubbed *Astrodon*, *Pleurocoelus*, and *Ornithopsis*, and come mostly from "small" sauropods. Today we know, however, that the features that make these remains "brachiosaurid-like" are present across several macronarian lineages, so the affinities of these taxa are not yet entirely clear.

Studies published since 2010 have established the existence of a revised Brachiosauridae, the oldest members of which (*Vouivria* from France) are from the Middle Jurassic while the youngest (*Sonorasaurus* from the USA) are from the Early/Late Cretaceous boundary. They're mostly North American and European, though the clade was obviously present in Africa too. What might be a South American brachiosaurid (*Padillasaurus* from Colombia) was reported in 2015, though its affinities are controversial.

See also Macronarians; Morrison Formation; Tendaguru.

Brontosaurus

One of the most famous and iconic of dinosaur names, associated with a specific taxon (*Brontosaurus excelsus*, named by Othniel Marsh in 1879), but also with a cultural icon, "the Brontosaurus" being a nondescript sauropod that appears in cartoons and films, and as a toy, trademark, or stereotype of what dinosaurs are like.

Brontosaurus was initially named for a Morrison Formation diplodocid discovered at Como Bluff, Wyoming. In 1903, Elmer Riggs argued that *B. excelsus* was sufficiently similar to the species included within an earlier

named Morrison diplodocid—*Apatosaurus*, also named by Marsh—that it should be absorbed into that same genus. Most experts agreed, and Marsh's name *Brontosaurus* mostly disappeared from the technical literature post-1903. It did not, however, disappear *entirely*: William D. Matthew used it in 1905 and Riggs himself used it several times in the 1930s, perhaps showing that he wasn't as confident about his 1903 decision as usually implied. More importantly, the name remained attached to a skeleton on display at the AMNH in New York, probably because the paleontologist in charge there—the bombastic Henry F. Osborn—wanted the world to know that he had his own take on Morrison sauropod taxonomy. The fact that New York's biggest and most prominent sauropod fossil was labeled *Brontosaurus* meant that the name was forever destined to be impactful, and a huge number of popular books, articles, and so on used the name as if Riggs's work of 1903 never existed. Fast forward to the end of the twentieth century, and *Brontosaurus* was still one of the best known of dinosaur names.

Some people argued that the name was so embedded within popular culture that we should abandon efforts to follow the rules of zoological nomenclature and use it anyway. Such was argued in Bakker's *The Dinosaur Heresies*. This also explains the title of Stephen Jay Gould's 1991 book *Bully For Brontosaurus*. An alternative position is that *Brontosaurus* is a name of the past, associated more with *The Flintstones* or Sinclair Oil than cutting-edge science, and not especially beloved of those generations who'd grown up with full knowledge that *Brontosaurus* was a junior synonym, and one with

strong pre-Renaissance connotations at that (*Brontosaurus* is a fat, shapeless swamp-dweller, not a svelte, striding marvel we might be proud of).

But there were always whispers that *Brontosaurus* might one day come back from the dead. Wasn't it the case—a few heretics muttered—that apatosaurine species weren't all alike, that those once labeled *Brontosaurus* actually looked *different* after all? In a giant 2015 study of diplodocid phylogeny and anatomy, Emmanuel Tschopp and colleagues found exactly this. *Apatosaurus excelsus*—the type species for *Brontosaurus*—didn't group with the other *Apatosaurus* species, and belonged to an altogether different branch on the cladogram. The name *Brontosaurus* had to be reinstated as a result. Given that our taxonomic conventions reflect the results of our ever-evolving, constantly changing thoughts on how organisms are related to one another, this isn't a "last word," nor is there any such thing. Future studies may cause us to change our minds on apatosaurine taxonomy yet again. But—for now—*Brontosaurus* is back.

See also Robert Bakker; Diplodocoids; Morrison Formation; Sauropods.

Carcharodontosaurs

Mostly gigantic Cretaceous and Late Jurassic allosauroids associated with South America and Africa. Carcharodontosaurs were first recognized in 1931 when Ernst Stromer, working on material discovered in the Late Cretaceous Bahariya Formation of Egypt, proposed that *Carcharodontosaurus* and *Bahariasaurus* were close kin and deserved to be united in a

clade termed Carcharodontosauridae. Unfortunately, these fossils were destroyed during WWII and only illustrations survived. Experts who wrote about these dinosaurs in the following decades generally considered them allosauroids, perhaps intermediate between *Allosaurus*-like and *Tyrannosaurus*-like theropods.

In 1995, theropod specialist Oliver Rauhut argued that Stromer's mostly forgotten Carcharodontosauridae was worthy of recognition after all, and that it was close to *Allosaurus*. Unusual features of *Carcharodontosaurus* include a gnarly surface to the top of the snout, and teeth that don't curve backward as they typically do in theropods. These teeth are vaguely (very vaguely) like those of the great white shark *Carcharodon*, and explain the name Stromer chose. A skull from Morocco, published by Paul Sereno and colleagues in 1996, verified Rauhut's findings and affirmed the gigantic size of *Carcharodontosaurus*. This specimen was said to have a skull 1.6 m (5.25 ft) long and be 14 m (46 ft) long in total, measurements that would make it bigger than *T. rex*. The media's response was predictable. But the Sereno reconstruction almost definitely over-lengthened the snout.

The year 1995 saw the publication of a similar animal, this time from Argentina. World, meet *Giganotosaurus*, a dinosaur with a name annoyingly similar to *Gigantosaurus* (a defunct African sauropod). This animal was also gigantic, and also touted as "bigger than *T. rex*." By now it was clear that Late Cretaceous South America and Africa were both home to gargantuan allosauroids, and that carcharodontosaurids were an important group of the Gondwanan continents. But were they limited

to Gondwana? What about *Acrocanthosaurus* from the Early Cretaceous of the USA? Named in 1950 and always considered related to *Allosaurus*, it appears to be a carcharodontosaurid too, albeit outside the clade that contains the southern taxa. The Chinese *Shaochilong* also appears to be a Northern Hemisphere carcharodontosaurid outside the Gondwanan clade, and additional taxa named since demonstrate the presence of carcharodontosaurids in Europe as well.

In his 1998 description of a new *Acrocanthosaurus* specimen, Jerry Harris noticed that *Neovenator* from the Wealden of southern England had enough carcharodontosaurid-like features to be considered another member of this clade. A 2010 study led by Roger Benson proposed that allosauroids found worldwide—Argentina's *Aerosteon*, Australia's *Australovenator*, and Japan's *Fukuiraptor*—shared enough features with *Neovenator* for the whole lot to be classified together in a new clade—Neovenatoridae—which had a sister-group relationship with Carcharodontosauridae. Benson and colleagues proposed another name—Carcharodontosauria—for the Neovenatoridae + Carcharodontosauridae clade. A consequence is that the vernacular "carcharodontosaur" is ambiguous now, since it could refer to either Carcharodontosauria or Carcharodontosauridae. Also worth noting here is the Benson team's suggestion that another clade—the megaraptorans—are part of Neovenatoridae, and thus part of Carcharodontosauria too. This is controversial and I have more to say on it elsewhere in the book.

Carcharodontosaurian behavior was probably similar to that of other allosauroids; however, the giant

size and laterally compressed, straightened teeth of some taxa suggest that they preyed on especially big animals (sauropods?) and used a slicing bite different from that of other theropods. Possible evidence for social behavior comes from the association of seven individuals of *Mapusaurus*, a *Giganotosaurus*-like animal from Argentina. This *might* show that these animals lived in groups, in which case this one was overcome by some disastrous event. Tracks from Glen Rose in Texas appear to have been made by *Acrocanthosaurus*, and a few parallel tracks *might* be evidence of social behavior too. But they might instead show that individuals walked in parallel through the area at different times. One of the Glen Rose tracks is said to show an acrocanthosaur approaching a sauropod, attacking it, and literally being lurched off its feet, since one of the tracks in the sequence is missing. This story has been challenged and one study has shown that the "missing track" isn't missing at all.

An interesting idea about carcharodontosaurian appearance was proposed in 2010 and pertains to the Early Cretaceous *Concavenator* from Spain. Bony nodes arranged in a line on the side of the ulna in the lower arm were suggested to be similar to the quill knobs of maniraptorans and thus show that these animals had feathers (or maybe modified, spikelike feathers or quills) projecting from the arms. I expressed skepticism about this in 2010. I think that the knobs are more likely something to do with muscles or internal fibrous tissue. There's been some debate about this and things remain unresolved. *Concavenator* is also interesting in

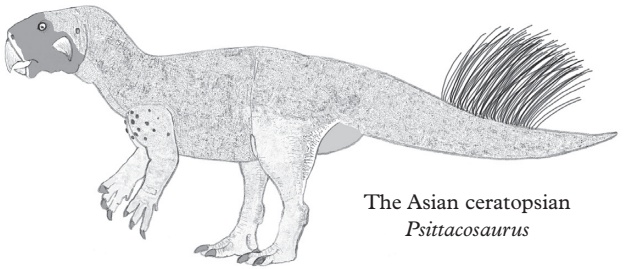
preserving large scales on its feet and the impressions of massive, bulbous toe pads.

See also Allosauroids; Megaraptorans.

Ceratopsians

The Jurassic and Cretaceous ornithischian clade (properly Ceratopsia and often called horned dinosaurs) that includes *Triceratops* and its kin. Ceratopsians are famously (albeit not universally) equipped with a bony frill at the back of the skull, and horns on the nose and above the eyes. *Triceratops* and its relatives—the most familiar of ceratopsians—are united within Ceratopsidae, a mostly North American clade whose species are rhino-like or elephant-like in size. Several other ceratopsian clades are less anatomically remarkable. These demonstrate the main evolutionary trend across the clade: they changed from small, bipedal forms to mid-sized and ultimately gigantic quadrupeds with large, frill-bearing, ornate skulls equipped with enlarged beaks and tooth batteries incorporating complex teeth.

The oldest and least anatomically modified ceratopsians include the chaoyangsaurids of Late Jurassic China (and perhaps Early Cretaceous Germany) and the psittacosaurs of Early Cretaceous eastern Asia. The members of these clades are 1–2 m (3–6.5 ft) long and bipedal. They didn't have frills or horns, but their skulls are broad across the cheeks and equipped with a narrow, hooked beak where an extra bone—the rostral—helped enlarge and provide mechanical support for the beak in the upper jaw. The best known archaic ceratopsian is *Psittacosaurus*, a dinosaur known from hundreds



The Asian ceratopsian *Psittacosaurus*

of specimens that belong to more than 10 species. These come from sediments deposited over a period of around 20 million years, an atypically long time for a dinosaur taxon typically regarded as a genus.

Around 135 million years ago, psittacosaur-like ceratopsians gave rise to the clade Neoceratopsia. Early neoceratopsians—initially similar to psittacosaurs in size and shape—differed in having a short bony frill and a shallow snout. By around 110 million years ago, they had diversified and given rise to several additional clades, some of which evolved quadrupedality and large size. The leptoceratopsids—a mostly quadrupedal clade of Asia, North America and Europe—persisted to the end of the Cretaceous. Rather better known are the coronosaurians, archaic members of which include *Protoceratops* of eastern Asia. *Protoceratops*-like coronosaurians gave rise to midsized (as in, about 3.5 m [11.5 ft] long) quadrupedal forms like *Zuniceratops* from the southern US, the first ceratopsian to possess supraorbital horns. And *Zuniceratops*, in turn, appears close to the ancestry of the ceratopsids. There's enough to say about ceratopsids that they get their own section.

Most of ceratopsian evolution happened in Asia, but the clade appears to have moved in and out of North America during its history. If *Zuniceratops* really is close to ceratopsid ancestry, it might be that ceratopsids originated in North America. But another near-ceratopsid—*Turanoceratops*—is from Uzbekistan, so it's difficult to say. Did ceratopsians occur elsewhere? Suggestions that fragmentary fossils from South America and Australia might be ceratopsians have been made but can't be verified.

Tracks and the sediments in which their remains are found show that ceratopsians were terrestrial animals of forested places, though some (like *Protoceratops*) inhabited deserts. It's been suggested that some ceratopsians might have been amphibious, either because they're vaguely hippo-shaped, because their remains have been preserved in aquatic environments, or because the tall bony tail spines of certain species might have supported a fin. These claims rely on the picking of one or two bits of evidence and the ignoring of others. It isn't beyond possibility that some ceratopsians were animals of watery habits but more study is needed before we can accept these ideas.

The wide, bulky bodies, shearing beaks and tooth batteries of ceratopsians show that they were herbivores of high-fiber plants, and they likely fed on plants that grew within 1–2 m (3–6.5 ft) of the ground. A fun idea which has enjoyed a bit of traction in the paleoart community is that ceratopsians might, on occasion, have exploited carcasses and chewed on bones, and it's possible that the smaller species were omnivorous. The narrow beaks, powerful jaws, and fierce appearance of these

dinosaurs makes it possible that they were formidable and aggressive, and able to put up a good fight should a predator fail to get the upper hand right away. This is, of course, wholly speculative; good luck demonstrating it scientifically.

One of the world's most remarkable fossils—dubbed the fighting dinosaurs and discovered in Mongolia in 1971—preserves a *Protoceratops* and *Velociraptor* locked in combat. Both seem to have died after being buried by sand. The *Velociraptor*'s left hand is hooked over the *Protoceratops*' face while its left foot is wedged against the ceratopsian's neck. But the *Protoceratops* has the *Velociraptor*'s right arm in its mouth and is in a crouching pose over the *Velociraptor*, so it isn't obvious that the *Velociraptor* has the upper hand, no pun intended.

Experts have disagreed on the speed and agility of these animals. All ceratopsians smaller than sheep were likely swift runners, but this is less clear for the big ones. Bakker argued in his writings of the 1970s and 80s that *Triceratops* had the bone strength, muscle and tendon size, proportions, and degree of limb movement to allow galloping, and his 1971 illustration of a galloping *Chasmosaurus* pair is an iconic image of the Dinosaur Renaissance. More recent efforts to test these claims have found that a fast run or trot was possible, but that galloping a la Bakker is not likely.

Finally, what about the function of those frills and horns? These massive, flamboyant structures surely evolved primarily as signaling structures or for use in combat, perhaps during the mating season. They might *also* have had roles in predator defense, heat-dumping, tree-breaking, or whatever, but their evolution was

driven mostly by the pressures of sexual selection, just as with antlers, antelope horns, peacock tails, and chameleon casques. Scars, pits, and broken horn tips confirm that ceratopsids fought with their horns and frills.

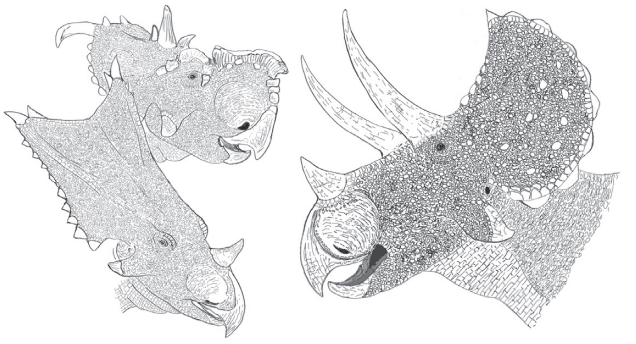
A particularly excellent book that reviews our knowledge of ceratopsians and the history of research on them is Peter Dodson's 1996 *The Horned Dinosaurs*.

See also Ceratopsids; Marginocephalians.

Ceratopsids

The largest, most diverse ceratopsian clade, and the one that includes the big, long-frilled, long-horned taxa like *Styracosaurus*, *Chasmosaurus*, and *Triceratops*. *Triceratops* and a few related kinds were truly gigantic, in cases reaching 9 m, 10 tonnes (29.5 ft, 11 tons), and with skulls more than 2.5 m (8 ft) long. Ceratopsids are almost entirely North American, with one exception, discussed below. Ceratopsid frills are fantastically variable, differing in size and shape and also in the form, number, and position of projections around their edges, and along the midline and apex.

Ceratopsids underwent major diversification in North America, their most notable evolutionary event being the split into the short-frilled, short-faced Centrosaurinae and long-frilled, long-faced Chasmosaurinae at around 80 million years ago. Centrosaurines generally lack horns over the eyes (termed supraorbital horns), while chasmosaurines generally have long ones. The existence of these two clades was recognized by the early 1900s, but *Triceratops*—one of the first ceratopsids to be discovered and named—was always controversial, since it has a short frill like a centrosaurine but a long



Left to right: *Chasmosaurus*, *Pachyrhinosaurus*, *Triceratops*

face and long supraorbital horns like a chasmosaurine. The Late Cretaceous *Pachyrhinosaurus*, notable for its hornlessness and presence of a massive nasal boss, was also controversial following its 1950 description. In studies of the 1960s and 70s, Wann Langston showed how *Triceratops* was an unusual member of Chasmosaurinae while *Pachyrhinosaurus* was an unusual member of Centrosaurinae. Studies published from 1990 onward have supported this work.

Since about 1994, a veritable cascade of new discoveries have added new branches and complexity to both the centrosaurine and chasmosaurine clades. Several discoveries show that centrosaurines started their history with long supraorbital horns, something we suspected given that ceratopsians close to ceratopsid ancestry—like *Zuniceratops*—have long supraorbital horns too.

Just one ceratopsid is known from outside of North America. This is *Sinoceratops* from the Late Cretaceous

of China. Because it belongs to an otherwise exclusively North American clade (the centrosaurines), it appears to show that a single migration event—involving movement from the Americas into Asia—occurred in the clade's history. There is, however, the sneaking suspicion that it hints at a more complex history, and it may well be that more Asian ceratopsids await discovery.

See also Ceratopsians.

Ceratosaurs

A theropod group named for the horned Jurassic *Ceratosaurus* but argued at times to include the Triassic and Jurassic coelophysids, the Jurassic dilophosaurids, and the mostly Cretaceous abelisaurids and noasaurids. *Ceratosaurus* has been known since 1884. Some of its features (like its four-fingered hands and a row of bony nodules along the midline of its back) seem primitive, but others are advanced and birdlike. As a result, experts between the late 1800s and 1980s disagreed on its evolutionary position. Some allied it with megalosauroids, others with coelurosaurs, and others regarded it as an archaic theropod worthy of its own clade.

In his 1986 review of theropod phylogeny, Jacques Gauthier argued that *Ceratosaurus* and the abelisaurids belonged together with the coelophysids and dilophosaurids. The whole lot, he argued, were united by the presence of a bony shelf on the side of the thigh bone's upper end, and by the presence of facial horns or crests. Gauthier co-opted a name for the group which Marsh had published in 1884—Ceratosauria—and proposed that Ceratosauria was a clade, and the sister-group of Tetanurae. This idea is interesting, since it would mean

that there were two contemporaneous theropod clades that descended from the same ancestor, one (Ceratosauria) more archaic than the other and with a distinctive facial look. A tempting analogy made more than once is that ceratosaurs might be imagined as the "marsupials" of the theropod world and tetanurans as the "placentals," though don't overthink this as it becomes less defensible the more you analyze it.

More recent studies have, alas, failed to support Gauthier's view, and have instead found *Ceratosaurus* and abelisaurids to be closer to tetanurans than they are to coelophysids and dilophosaurids. Does this mean that we should abandon the name Ceratosauria? Well, maybe, but maybe not if a *Ceratosaurus* + abelisaurid clade exists, as some experts think it does. The fact that the name Ceratosauria has been used in different ways means, today, that any person using it has to explain which version of the term they have in mind.

Ceratosaurus was about 6 m (19.5 ft) long, and this in combination with its long teeth and large, deep skull show that it was a predator of large animals. The same was probably mostly true of the abelisaurids. Coelophysids (which were mostly 3–4 m [10–13 ft] long) were different, their shallow, narrow skulls and lightweight proportions suggesting they were predators of arthropods, small reptiles, and maybe fish. Dilophosaurids (6–7 m [19.5–23 ft] long) are built something like giant, heavily built coelophysids, and some experts have argued that this is exactly what they are. They're famous for their extravagant head gear. *Dilophosaurus* from the Early Jurassic of the southern USA has twinned, plate-like bony crests that might have been part of a larger, casque-like structure. *Cryolophosaurus* from the Early Jurassic of Antarctica has a vertical, fanlike crest formed of flattened, fingerlike bony projections above its eyes. Presumably these crests, horns, and other structures were used in display and communication, as are similar structures in modern birds and lizards.

See also Abelisaurids; Tetanurans.

Coelurosaurs

The enormous tetanuran clade that includes birds and other maniraptorans, ornithomimosaurs, and tyrannosauroids. The name Coelurosauria has a convoluted history which I can't begin to summarize here. But the modern concept of the term is rooted in Jacques Gauthier's proposal of 1986 that this name—first published by Friedrich von Huene in 1914—should be used for the clade containing all theropods closer to birds than to theropods like *Megalosaurus* and *Allosaurus*.

To Gauthier, this meant inclusion of the various small, agile theropods of the Late Jurassic—chicken-sized *Compsognathus* from Europe and *Ornitholestes* and *Coelurus* from the Morrison Formation—in addition to ornithomimosaurs and maniraptorans.

A series of studies published from the mid-1990s onward showed that tyrannosauroids should be included among this lot as well. Tyrannosauroids are substantially more birdlike than tetanurans like *Allosaurus* and must have evolved from small predators similar to *Coelurus*. In fact *Coelurus* (and other tetanurans of this sort) have always been imagined as the archetypal, ancestral coelurosaurs: as nimble, speedy, ground-running predators of the forest understorey, around 2 m (6.5 ft) long, equipped with long arms and three-fingered, grabbing hands. These *Coelurus*-like theropods were likely warm-blooded, so the idea that they might have been insulated by a feathery coat extends back to the 1970s. Fossils discovered since the 1990s have confirmed the presence of feathers on these animals, so feathers originated early in coelurosaur history, long before birds did. Presumably, their initial function was to retain heat, and only later did they become co-opted for use in flight and display.

At some point during the Early Jurassic (around 180 million years ago), some *Coelurus*-like coelurosaurs (certainly not *Coelurus* itself) evolved longer legs and necks and gave rise to ornithomimosaurs. Others began to rely on the strength of their jaws and teeth and were the earliest members of Tyrannosauroidea. Members of another lineage evolved longer arms and hands and smaller size and gave rise to maniraptorans. By the Late

Representatives of some of the major coelurosaurian groups

Jurassic, tens of coelurosaur species, representing numerous clades, inhabited the forests, prairies, deserts, and wetlands of the world, typically in environments where ceratosaurs, megalosauroids, and allosauroids were the big, dominant predators.

The Cretaceous might be imagined as the "Age of Coelurosaurs": those other theropod groups were still around, but it was coelurosaurs which had evolved to fill the largest variety of ecological niches, the greatest variation in body size, and the most profound variation in body and skull shape. A lucky observer exploring a Late Cretaceous habitat in North America or Asia might have seen giant, omnivorous ornithomimosaurs, great, terrifying tyrannosauroids, and such maniraptorans as coyote-sized dromaeosaurids, ostrich-sized oviraptorosaurs, gigantic therizinosaurs, and some considerable diversity of birds.

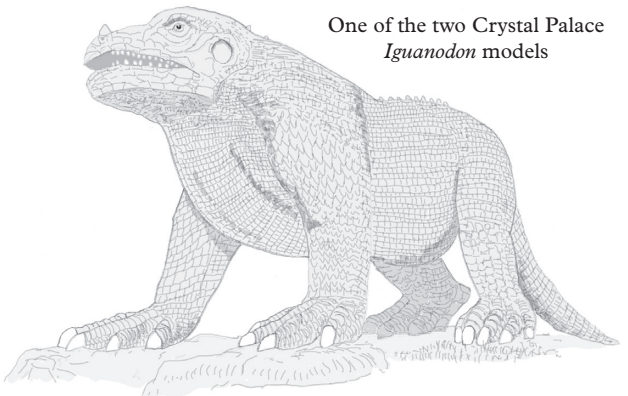
See also Maniraptorans; Ornithomimosaurs; Tetanurans; Tyrannosauroids.

Crystal Palace

The south London park located in Penge (not Sydenham, as used to be stated), famous for its life-sized prehistoric animal models, all of which were constructed during the early 1850s. The models were part of a well-funded outreach project designed to accompany the relocation of the Crystal Palace building from Hyde Park (where it formed part of the Great Exhibition of 1851) to its new home on Penge Common. A landscaped, geology-themed park incorporating lakes, fountains, wooded areas, and gardens was constructed, and the models were sited on islands. Crystal Palace Park

remains in use today, but its appearance and function have changed substantially. The palace building burned down in 1936.

The models depict the three founding members of Dinosauria—*Megalosaurus*, *Iguanodon*, and *Hylaeosaurus*—as well as ichthyosaurs, plesiosaurs, pterosaurs, a mosasaur, and various animals of the Paleozoic and Cenozoic. Naturally, they're portrayed as per knowledge of the time, such that *Iguanodon* is a rhinocerotine quadruped with a nose horn, *Megalosaurus* is a sort of bear-crocodile-elephant mashup, and *Hylaeosaurus* is an iguana-like creature with a row of spines. It has occasionally been said or implied that the models are hilariously out of date. In reality, they were up to the minute at the time of construction, and should more sensibly be described as accurate, faithful representations of the scientific knowledge of the time. Their design and construction are owed entirely



One of the two Crystal Palace *Iguanodon* models

to artist and sculptor Benjamin Waterhouse Hawkins, who was tasked with bringing to life the view of these animals described by Richard Owen. Owen gets credit as the scientific advisor, but exactly what role he played (beyond writing the guidebook) remains uncertain.

There's always been a modicum of historical interest in the Crystal Palace models. But only since the 1990s have those interested in artistic reconstructions of prehistoric animals paid detailed attention to their anatomy and the story of their construction. It's increasingly recognized that they're nuanced, fantastically detailed pieces of craftmanship. This interest has gone hand-in-hand with efforts to see them and their grounds restored, cared for, valued, and celebrated. 2020 saw the installation of a bridge allowing improved access for maintenance, but also the continuing deterioration and vandalism of the models, specifically the ripping apart of the *Megalosaurus*' face by a member of the great British public.

See also Richard Owen.

Deinonychus

Few non-bird dinosaurs can be considered as iconic as *Deinonychus antirrhopus*, a species named by John Ostrom in 1969 following discoveries made in the Lower Cretaceous Cloverly Formation of Montana, USA. Ostrom realized that *Deinonychus* was a member of Dromaeosauridae, a maniraptoran theropod clade named by William D. Matthew and Barnum Brown in 1922. Prior to Ostrom's work, dromaeosaurids were poorly understood and regarded as nondescript predators shaped like miniature tyrannosaurids.

Matthew and Brown actually regarded dromaeosaurids as a subgroup within Deinodontidae, this being their favored name for Tyrannosauridae.

Ostrom described *Deinonychus* as a midsized predator (it was around 3.5 m [11.5 ft] long and 60 kg [132 lbs]) with long hands, a flexible, birdlike wrist, a tail kept stiff by intertwined bony rods, and powerful hind limbs in which the second toe was arranged such that its enormous, strongly curved claw—the sickle claw—was kept raised off the ground. It was this claw which led Ostrom to give *Deinonychus*—meaning "terrible claw"—the name he did. He suggested that the sickle claw was a disemboweling weapon which *Deinonychus* deployed while standing on one leg and kicking with the other. Behavior of this sort requires agility and excellent balance, so here was evidence that some dinosaurs were dynamic, sprightly, hot-blooded predators. Robert Bakker's illustration of *Deinonychus* in mid-stride, produced to accompany Ostrom's 1969 description of this dinosaur, helped put it front and center in every discussion of the Dinosaur Renaissance.

Because the remains of several *Deinonychus* individuals had been discovered together, Ostrom further proposed that *Deinonychus* was a group-living pack-hunter that ganged up to kill big dinosaurs, the rhino-sized ornithopod *Tenontosaurus* being—in his view—*Deinonychus*'s most favored item of prey.

Today we know that Ostrom wasn't, actually, the first to "discover" *Deinonychus*. Bones of the exact same animal were discovered by Barnum Brown and Peter Kaisen on an American Museum of Natural History expedition of 1931, and Brown went as far as having a skeletal reconstruction prepared for a planned publication. His working name for this animal was *Daptosaurus agilis*. But, alas, he never got around to finishing this work . . . a problem that any working scientist knows all too well.

Deinonychus hasn't become notably better known since the publication of Ostrom's 1969 monograph, bar the appearance of new work on its palate, snout shape, and hand orientation. Dromaeosaurid fossils from China show that dromaeosaurids large and small were fully feathered, with a plumage much like that of *Archaeopteryx* and other archaic birds. Their forelimbs were winglike and oriented such that the palms were fixed in an inward-facing pose. All these things would have been true of *Deinonychus*. It would have looked more like a giant, striding, long-tailed hawk than anything else.

Ostrom's views on the behavior and lifestyle of this dinosaur have also undergone revision. Sickle-shaped claws aren't, it turns out, built for slicing or slashing at giant animals, but for gripping or pinning small ones.

Ostrom's view that *Deinonychus* was a pack-hunter has been the source of considerable debate. Some experts have outright stated that group hunting wasn't likely for these animals (it's more of a mammalian habit than a reptilian one, so the argument goes), nor is it well supported by geological data, since the individuals Ostrom regarded as members of a social group more likely came together by accident (they were washed together by floodwater, say). But none of this appears exactly right; social behavior is reasonably well supported in these animals and can't be easily explained away, *Deinonychus* isn't the only dromaeosaurid where several individuals have been discovered in association, and the diversity of group-hunting strategies present in modern lizards and birds shows that cooperation and group living are far from "mammal-only" behaviors. It's plausible that *Deinonychus* sometimes hunted alone, but it's also likely that individuals stalked and foraged in bands, cooperated in the flushing and pursuing of prey like small ornithischians, and slept and nested in groups.

See also Robert Bakker; Dinosaur Renaissance; John Ostrom; Maniraptorans; Raptor Prey Restraint.

Dinosaur Renaissance

The cultural event of the 1960s and 70s (though read on) in which dinosaurs were recast as agile, social, warm-blooded, successful animals that live on as birds. Those promoting this view of dinosaurs—predominantly John Ostrom and his student Robert Bakker—disputed the stereotype prevalent beforehand: that dinosaurs were monuments of inefficiency and bad design, destined for extinction. Bakker termed this overturning of ideas

a Renaissance, his argument being that it marked a return to a more vigorous view of dinosaurs prevalent during the late 1800s.

The Renaissance made dinosaurs attractive areas of discussion, and heated exchanges on their biology occurred in scientific journals. Adrian Desmond's 1975 book *The Hot-Blooded Dinosaurs* did much to popularize the Renaissance, as did articles in *Scientific American*, *National Geographic*, and *Discovery*.

The Dinosaur Renaissance is usually implied to result from Bakker's and Ostrom's efforts alone, the main catalysts being Bakker's articles (published between 1968 and 1974) on dinosaur "warm-bloodedness" and the terrestrial lifestyle of sauropods, and Ostrom's 1969 description of *Deinonychus*. But an alternative take on the Renaissance might be that it was the inevitable consequence of post-WWII history and generational turnover. The ideas Ostrom and Bakker promoted were based mostly on fossils—like those discovered during the Polish-Mongolian expeditions of the 1960s and 70s—whose discovery and study could only happen within the decades following WWII. Furthermore, the postwar baby boom resulted in the existence of a generation the right age to be intrigued by, and engage with, the implications of these fossils. Such topics as the origin of birds, dinosaur behavior, and dinosaur feeding mechanisms had *always* been the topic of investigation, it's just that the number of studies published prior to the 60s and 70s had been low due to a small number of publishing paleontologists. Take all of this into consideration, and a fairer appraisal of the Renaissance might be that it occurred as a perfect storm of events.

If the Renaissance was a cultural "event," when did it end? Was it short-lived and ended during the 70s, was it more drawn-out, or is it that we're still in it? I invited the thoughts of colleagues on this matter and discovered a diversity of opinions. The fact that we remain in a dynamic, fast-moving period whereby the ideas of the Renaissance continue to be supported and investigated *could* mean that the Renaissance is still ongoing.

But I rather prefer the view that the Renaissance could be considered "finished" once Renaissance views of dinosaurs became accepted in mainstream culture. The 1993 appearance of *Jurassic Park* could be interpreted as marking that acceptance, as could the 1990s publication of feathered dinosaurs like *Sinosauropteryx* and *Caudipteryx*. And if the Renaissance *has* finished, maybe we're now in a new period, a sort of *Dinosaur Enlightenment*.

See also Robert Bakker; *Deinonychus*; John Ostrom.

Dinosauroid

The idea that life on Earth might be very different had non-bird dinosaurs not died out is a familiar staple of science fiction. But it's one that's also been explored by scientists and science writers. From 1969 onward, Canadian paleontologist Dale Russell (1937–2019) published a series of papers on troodontids, a group of maniraptorans notable for their proportionally large brains (well, large for non-bird dinosaurs). Russell was especially interested in the evolution of intelligence, the possible existence of alien life, and the Search for Extraterrestrial Intelligence (or SETI) project.

What, he wondered, might troodontids look like had they not become extinct 66 million years ago? Russell explored this speculation in a 1982 article, coauthored with Canadian Museum of Nature model maker and taxidermist Ron Séguin. Séguin had been tasked with the construction of a life-sized model of a troodontid, and through collaboration with Russell he also built a hypothetical troodontid descendant. Russell and Séguin proposed that troodontids would have evolved a larger brain had they persisted beyond the Cretaceous, and that this would have led to an erect posture, reduced tail, and humanoid form. They called the resulting creature the dinosauroid.

Feelings on the dinosauroid have run in two directions. On the one hand, there are those who've argued that convergent evolution is so pervasive, and the human form so effective a design, that the evolution of humanoid dinosaurs is plausible, perhaps even likely or inevitable. Such has been promoted by evolutionary scientists and authors Simon Conway-Morris and

Richard Dawkins. On the other hand, another group (mostly paleontologists who specialize in dinosaurs) have argued that Russell's underlying premise—that troodontids would become humanoid had they evolved larger brains—is flawed, since a big-brained maniraptoran would remain maniraptoran-like, not head in a humanoid direction of evolution.

Dinosauroid-like creatures had been portrayed innumerable times before Russell and Séguin's project. Examples include the Mahars and Horibs of Edgar Rice Burroughs' writings, the Silurians of *Doctor Who*, and the Sleestaks of *Land of the Lost*. There is, however, no indication that any of these were inspirational to the dinosauroid. Others appeared afterward, sometimes as homages, but sometimes (as with Harry Harrison's Yilané from 1984's *West of Eden*) to show that the author could portray more "plausible" smart reptiles. Since about 2014, numerous artists have invented their own "dinosauroids," most of which are feathery, horizontal-bodied animals which more resemble maniraptorans than scaly green humanoids.

There are indications that Russell was unhappy with the mostly negative reception the dinosauroid received, and it might be that it damaged his credibility. However, the primary aim of the project was to encourage discussion of the idea that the humanoid form could be evolved by other forms of life, the concluding words of his and Séguin's 1982 paper being "We invite our colleagues to identify alternative solutions." Seen from this point of view, the experiment was a major success. The dinosauroid has remained a touchstone of discussions

on speculative evolution, numerous copies of Séguin's model exist, and few people interested in dinosaurs are unaware of it.

See also Maniraptorans.

Diplodocoids

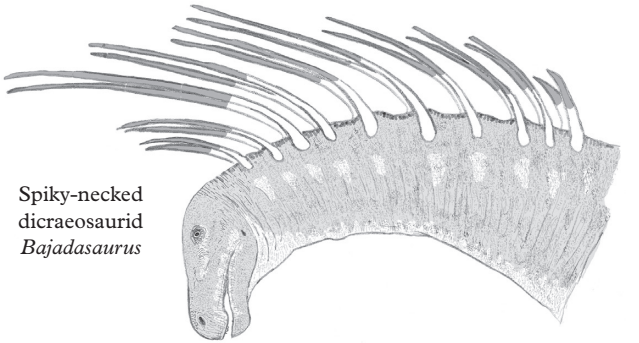
The sauropod clade which includes the archaic rebbachisaurids and the whip-tailed dicraeosaurids and diplodocids. Key features uniting all three include slender tooth crowns and short, non-overlapping ribs on the neck vertebrae. A typical diplodocoid has an especially long neck and tail, and a lightweight, long, shallow-snouted skull with a squared-off mouth. The skulls of some rebbachisaurids are unusual in that the end of the snout is the widest part, and the only part to contain teeth. The whiplike tail tips of dicraeosaurids and diplodocids likely served an offensive or defensive function.

The best known diplodocoids are the Morrison Formation animals *Diplodocus*, *Barosaurus*, *Apatosaurus* and *Brontosaurus*, all of which belong to Diplodocidae. They include some of the largest of dinosaurs, some exceeding 25 m (82 ft) in length. Possibly even bigger is *Maraapunisaurus*, also of the Morrison Formation. Its now lost remains suggest a length of more than 30 m (98 ft). *Maraapunisaurus* was long regarded as a diplodocid but has recently been reidentified as a rebbachisaurid.

A few aspects of diplodocoid biology and behavior remain the topic of argument. The presence in diplodocids of relatively short forelimbs, tall vertebral spines in the hip region, and an aft-located center of mass (plus

other features) have led some researchers to argue that members of this specific group were good at standing in a bipedal or tripodal pose. Maybe they did this to reach high up into foliage, when fighting, or when intimidating or battling big theropods. The habitual neck pose of these animals is also debated. Some researchers argue that diplodocoid necks were constrained to a horizontal pose, perhaps with an upward or even downward curve at the head end, while others (including myself) think that the necks were ordinarily held mostly erect. Add these things together and we come to a third area of argument: feeding behavior. Did diplodocoids use their ultra-long necks to reach down to the ground to crop ferns, horsetails and cycads, or were they more adept at reaching up, beyond the reach of other herbivores and into the canopy? My take is that they were doing both of these things as and when required, their behavior changing from one species to the next as well as across their life span. Claims that erect neck poses would be disallowed by blood pressure are naive given that the sauropod neck—a structure some order of magnitude bigger than that present in living animals—almost certainly involved the existence of remarkable soft tissue specializations.

Diplodocoids are associated mostly with the Late Jurassic; however, the Chinese dicraeosaurid *Lingwulong* shows that they'd diversified into their three major groups prior to the Middle Jurassic. Despite this, rebbachisaurids are predominantly Cretaceous (*Maraapunisaurus* being an exception). The relatively short necks, downcurved snouts, and wide mouths of rebbachisaurids might show that they were specialized ground-level



Spiky-necked dicraeosaurid *Bajadasaurus*

feeders. Both diplodocids and dicraeosaurids persisted into the Cretaceous in South America, and among the last of them were the remarkable dicraeosaurids *Bajadasaurus* and *Amargasaurus*, both of Argentina. Long bony spines, projecting upward from the neck vertebrae, were probably sheathed in horn and perhaps used in visual display.

See also *Brontosaurus*; Morrison Formation; Sauropods.

Hadrosaur Nesting Colonies

By the 1970s, it was well established that non-bird dinosaurs constructed nests where they deposited their oval or near-spherical eggs. This was demonstrated by fossil eggs and nests found in various locations, most famously those found during the 1920s in the Late Cretaceous rocks of Mongolia. There were, however, no clear ideas on whether non-bird dinosaurs practiced parental care, whether their nesting was a solitary or social affair, or whether they had a preference

with respect to the nesting sites they chose. The fact that Mesozoic dinosaur eggs and nests were rare led to the belief that nesting behavior was restricted to upland places, but why babies were so rare remained enigmatic.

This changed during the late 1970s and throughout the 80s as studies led by Jack Horner announced a series of finds made in western Montana, USA. In 1978, Horner and his friend and colleague Bob Makela visited the small Montana town of Bynum. At a rock and fossil shop owned by Marion Brandvold, they were asked to identify some small bones. These turned out to be baby hadrosaur bones from an animal around 45 cm (1.5 ft) long, the first of a string of amazing discoveries.

The bones came from the sediments of the Two Medicine Formation, a Late Cretaceous layer about 77 million years old. After exploring the exact spot where Brandvold had found them, Horner and Makela discovered a bunch more (representing another 14 individuals), all jumbled together, preserved in what had originally been a circular depression on top of a mound. Eggshell fragments were associated with the bones. This was a hadrosaur nest, and the remains belonged to a new kind of hadrosaur, which they named *Maiasaura* (meaning "good mother lizard") in 1979. The skull of an adult was found about 100 m (328 ft) away. Because the babies had died in the nest, Horner and Makela proposed that parental care existed, but that this unfortunate lot had starved to death after one or both parents failed to return.

In subsequent studies, Horner reported the presence of an additional six or so *Maiasaura* nests at the same site, all spaced around 7 m (23 ft) apart. Here was

evidence that this hadrosaur—and presumably hadrosaurs in general—nested in colonies. The timing of these discoveries was ideal, since they were announced while writers and journalists were still reeling from the implications of the Dinosaur Renaissance. Here was evidence that non-bird dinosaurs were behaviorally complex and even birdlike in breeding behavior. The consequence is that *Maiasaura* gets its own section in virtually every single post-1979 book or article on dinosaurs, and that *Maiasaura* and its cute, short-snouted babies are among the most frequently illustrated of all hadrosaurs.

Horner's model for nesting and parental behavior in *Maiasaura* is that these animals gathered in colonies to nest, constructed crater-shaped nests in which a clutch of 20–30 eggs were incubated by rotting vegetation, that one or both parents brought food to the hatchlings, and that the hatchlings stayed in the nest until they were around 1 m (3 ft) long. Subsequent discoveries made elsewhere—including other locations in Montana and Devil's Coulee in Alberta, Canada—have supported this model of colonial nesting and parental care, and in fact colonial nesting has since been documented for sauropods and non-bird theropods too.

See also Dinosaur Renaissance; Hadrosaurs; Jack Horner.

Hadrosaurs

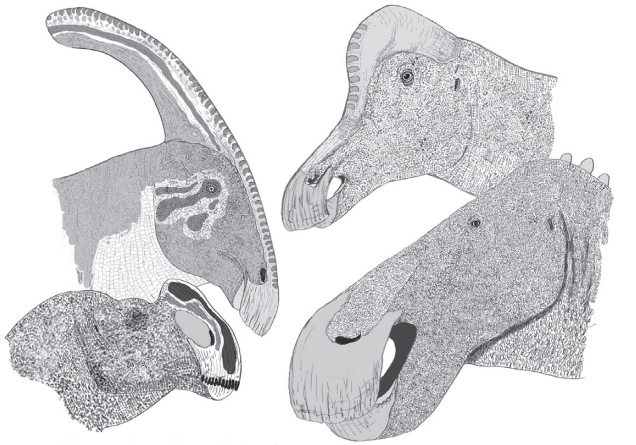
Among the most abundant, widespread, and best understood of non-bird dinosaur clades. Hadrosaurs—often termed duck-billed dinosaurs or duck-bills (though read on)—are a mostly Late Cretaceous clade

of iguanodontian ornithopods. They belong to a larger group (termed Hadrosauroidea) which evolved from big, *Iguanodon*-like quadrupeds.

Hadrosaurs were mostly large or very large herbivores, species ranging from 4 m (13 ft) to an incredible 17 m (56 ft) in the gigantic *Shantungosaurus* of eastern China. They were equipped with robust hind limbs with three-toed feet, a muscular tail that was stiff and shallow in its end half, and specialized hands where the thumb was absent, the middle three digits were united in a pseudohoof, and the fifth finger was rodlike and independently mobile. The hadrosaurian skull combines a toothless, beaked region with massive tooth batteries. Their teeth, cemented together for strength, underwent constant replacement. Around 1,000 teeth were present in some species, and histological work shows that they're among the most complex teeth that have ever evolved.

Hadrosaurs are diverse in skull anatomy. There are long-faced, crestless taxa, those with deep, arched nasal regions, a clade with solid, spike-shaped bony crests and another with hollow bony crests that have a complex architecture. One fossil seems to show that even taxa lacking bony crests might have had soft, fleshy crests. Dismissive claims that hadrosaurs are all the same bar skull shape are dead wrong: there's considerable variation in their proportions, limb bone shapes and much else.

Within recent decades, the consensus has been to regard hadrosaurs as a clade (termed Hadrosauridae) that contains two additional, internal clades: the flat-headed and solid-crested Hadrosaurinae, and the hollow-crested Lambeosaurinae. Additional



subdivisions within both of these clades have been recognized as well. Within Hadrosaurinae, the clades Brachylophosaurini, Edmontosaurini, Kritosaurini, and Saurolophini are recognized. Meanwhile, Lambeosaurinae contains Aralosaurini, Tsintaosaurini, Parasaurolophini, and Lambeosaurini.

A complication arose in 2010, however, when hadrosaur expert Alberto Prieto-Marquez discovered that *Hadrosaurus* from New Jersey—the namesake member of the group (and among the first of North American non-bird dinosaurs to be named)—belongs outside the clade that contains most other hadrosaurs. This means that the name Hadrosaurinae can't be applied to the group conventionally given that name. Saurolophinae (originally published in 1918) is available as an alternative, and Prieto-Marquez and his colleagues endorse the use of "saurolophine" in place of "hadrosaurine."

Another complication worth mentioning is Jack Horner's idea, proposed during the early 1990s, that saurolophines and lambeosaurines have distinct ancestry and that the former descend from *Iguanodon*-like ancestors, while the latter evolved from *Ouranosaurus*-like animals (*Ouranosaurus* is a sail-backed iguanodontian from the Early Cretaceous of Niger). This hasn't been supported by more recent studies.

The flattened, broad snout of saurolophines like *Edmontosaurus* explains why these dinosaurs have often been described as "duck-billed" ("spoon-billed" has also been used). Hadrosaurs like *Edmontosaurus* do, it's true, have a skull that looks spatulate when viewed from above or below. But exceptional specimens with their keratinous beak tissue preserved show that this spatulate anatomy was obscured in life, and that a massive down-curved bill was instead the dominant feature. This configuration was correctly described by Jan Versluys in 1923 and again by William Morris in 1970 but mostly ignored until recently.

This massive bill was used in cropping foliage of all sorts. When we combine its anatomy with that of the tooth batteries, it appears that hadrosaurs were unstoppable, incredible destroyers of plants, able to break apart and consume leaves, fronds, stems, branches, and even wood. A diet involving all these items—as well as occasional animal matter, like crustacean parts—is confirmed by fossil hadrosaur dung. An old-fashioned idea that hadrosaurs were amphibious and limited to a diet of soft water-plants therefore has a lot counting against it. It does, however, remain possible that hadrosaurs were good waders or swimmers, and it might be that

some taxa consumed amphibious or aquatic plants on a regular basis. But hadrosaur anatomy shows mostly that they were terrestrial animals of wooded places and even scrub and semidesert. When it comes to other aspects of biology, we know much about hadrosaur nesting behavior thanks to eggs, nests, and nesting grounds discovered in the USA.

Hadrosaurs are associated mostly with North America and Asia, but taxa are also known from South America, Europe, Antarctica, and northern Africa. This distribution is consistent with a mid-Cretaceous origin in eastern Asia followed by a series of dispersals to other regions, some of which likely involved over-water crossings (or swimming, as it's more generally known).

See also Hadrosaur Nesting Colonies; *Iguanodon*; Ornithopods.

Hell Creek

Among those locations associated with dinosaur-bearing sedimentary layers, few are as famous as Hell Creek, Montana. Why? Well, hold on, we'll come to that in a minute. Hell Creek is characterized by badlands topography, a landscape where dry gullies and steep slopes have formed by wind and water erosion. The sediments here—consisting of mudstones, siltstones, and sandstones—date to the Late Cretaceous and Paleocene, but it's the Cretaceous layers that are of direct interest to us. They're from the Maastrichtian (the very final geological stage of the Late Cretaceous) and belong to a set of sediments that extend over part of North and South Dakota and Wyoming in addition to Montana.

Famous paleontologist Barnum Brown was the first to recognize these sediments as worthy of a name: in 1907, he named them the Hell Creek beds. But in the years that followed, experts mostly regarded the Hell Creek sediments as part of the Lance Formation. The term Hell Creek Formation came into use during the 1950s but wasn't formally established until 2014. The terms Hell Creek and Hell Creek Formation are not technically synonymous, but it's common in discussions of Late Cretaceous life to refer to all the animals of the Hell Creek Formation as belonging to the Hell Creek fauna.

The main reason for Hell Creek's fame comes from the fact that this is the area in which the *Tyrannosaurus rex* holotype (the key specimen regarded as the one associated with the name) was discovered back in 1902, though it has to be said that the memorable name is surely a factor as well. "Hell Creek" is fitting for a place associated with an animal often regarded as the world's most awesome apex predator. In addition to *T. rex*, the Hell Creek fauna includes *Triceratops*, *Ankylosaurus*, *Pachycephalosaurus*, and the hadrosaur *Edmontosaurus*, all of which can be considered the final, "ultimate" members of their respective clades.

But it's not all dinosaurs. Plant fossils provide a good impression of what the place was like during Maastrichtian times, and numerous fishes, amphibians, mammals, lizards, turtles, and invertebrates are known from Hell Creek sediments too. This was a densely forested, subtropical or temperate lowland during the Maastrichtian, with a hot rainy season and cool dry season. Animals like *T. rex* stalked forests and fern prairies, but swamps

and rivers occurred in the region and the area was entirely swampy at times. The proximity of the receding Western Interior Seaway meant that estuarine conditions were present to the south and east, and marine animals sometimes entered local rivers.

The significance of the Hell Creek Formation to the study of Mesozoic geology and paleontology is reflected by the fact that the Hell Creek Fossil Area was designated a National Natural Landmark by the National Park Service in 1966. Fieldwork in Hell Creek continues today, and work on its fossils, sedimentology, and stratigraphy appears regularly in the scientific press. Furthermore, its animals, plants and environments are unusually well represented in paleoart, and artists have gone to considerable trouble to portray things accurately.

See also *Tyrannosaurus rex*.

Herrerasaurs

One of the most archaic dinosaur groups, a predatory, theropod-like clade of Late Triassic South America, and probably North America, Europe, and India. Herrerasaurs (properly Herrerasauridae) became known in 1973 when *Herrerasaurus* was described from Argentina. It was initially suspected to be a prosauropod. Excellent remains described in the 1990s show that *Herrerasaurus* had a rectangular snout, long, recurved teeth, and theropod-like forelimbs. Large claws are present on the inner three fingers, and the mobility of the wrist and elbow is similar to that of tetanurans. *Herrerasaurus* is the largest member of the clade, in cases reaching 6 m (19.5 ft). Other herrerasaurs—they include

Sanjuansaurus from Argentina and *Staurikosaurus* and *Gnathovorax* from Brazil—were 2–3 m (6.5–10 ft) in length.

The herrerasaur pelvis is odd (the pubic bone projects straight downward, rather than down and forward as it "should"), the foot is broad relative to the theropod one, and there appear to be just two sacral vertebrae (as opposed to three, supposedly the minimum number for dinosaurs). For these reasons (and others), one of the most popular views on herrerasaurs is that they're archaic saurischians outside the theropod + sauropodomorph clade. Another is that they're archaic dinosaurs outside the Saurischia + Ornithischia clade. Yet another is that they should be excluded from Dinosauria altogether and regarded as "near-dinosaurs."

A new and surprising view on herrerasaurs was published in 1993 when Paul Sereno and colleagues described *Eoraptor*, an archaic dinosaur from the Late Triassic of Argentina. Here, it was argued that herrerasaurs were archaic theropods, and that the anatomy of the herrerasaur jaw, hand, shoulder blade, and tail was more theropod-like than credited in previous studies. Sereno has continued to make this point in more recent work and has drawn attention to additional theropod features in the herrerasaur palate and face. Sereno has also argued that herrerasaurs possess three sacral vertebrae, not two. Finally, where does the Ornithoscelida model place herrerasaurs? The studies concerned have found herrerasaurs to form a clade with sauropodomorphs, a view recalling the original one favored back in the 1970s.

So far as we know, herrerasaurs were restricted to the Late Triassic, and it appears that they died out prior to the Triassic-Jurassic boundary. Other than the fact that they were terrestrial and predatory (and presumably preyed on other dinosaurs, as well as on other contemporary animals), nothing is known of their biology or behavior.

See also Ornithoscelida; Paul Sereno; Theropods.

Heterodontosaurids

A group of small, lightly built, bipedal ornithischians notable for their canine-like fangs. The namesake member of the group—*Heterodontosaurus* from the Early Jurassic of South Africa and Lesotho—was named for its heterodonty (that is, its possession of different tooth types), since its has incisor-like, canine-like, and molar-like teeth. There are toothless, beaked regions at the front of the upper and lower jaws, too. The arms are long; the three inner fingers on the five-fingered hands are also long and have large, curved claws. The hind limbs are long, and some of the bones are fused together, so these dinosaurs were swift runners. *Heterodontosaurus* was a large heterodontosaurid, perhaps exceeding 1.5 m (5 ft). Most were around 1 m (3 ft) or less. *Echinodon* from the Early Cretaceous of England—one of several taxa which show that the group persisted into the Cretaceous—was 60 or 70 cm (ca. 2 ft), and *Fruitadens* from the Morrison Formation was small, too. These are the smallest known ornithischians.

Heterodontosaurus was a desert dweller, and some other heterodontosaurids were, too. But they're also

known from places where subtropical and temperate woodlands and savanna-like habitats occurred. Their fossils come from South and North America, Africa, Europe, and Asia, but the fact that they originated at a time when the continents were united could mean that they were cosmopolitan.

The presence of fanged and non-fanged heterodontosaurids in sediments of similar age has led some to argue that these are sexual dimorphs of the same species,

and that males used their fangs in fighting and display. We currently think that fanged and fangless specimens belong to different taxa because they differ in numerous ways, not just in whether they have fangs. Furthermore, a juvenile *Heterodontosaurus* has prominent fangs, which also counts against a sociosexual role. In 1978, paleontologist Tony Thulborn argued that heterodontosaurids didn't undergo continuous tooth replacement, that their teeth could only have been replaced during a single event, and that aestivation (a dormant period occurring during the dry season) provided the answer. Alas, newer study has revealed copious evidence for tooth replacement within the group and no reason to think that they aestivated. Because heterodontosaurids are ornithischians, it's been assumed that they were herbivorous, and their tooth wear is consistent with this. The possibility exists that they were omnivorous or even predatory, however.

Where do heterodontosaurids fit in the ornithischian family tree? The position favored during the 1970s, 80s, and 90s was that they're archaic ornithopods, a view popular at a time when "ornithopod" was synonymous with "bipedal ornithischian." But they lack traits of Ornithopoda proper, so this view is no longer supported. Several studies have found heterodontosaurids to be one of the oldest clades within Ornithischia as a whole, potentially close to the group's common ancestor. If this is so, their long arms and hands and leggy, long-tailed gestalt could reflect an evolutionary closeness to early theropods and sauropodomorphs. Indeed, a similarity between heterodontosaurids and theropods helped inspire the Ornithoscelida hypothesis.

Heterodontosaurids are also marginocephalian-like in the form of their teeth, skull, and hips. As a result, an idea mentioned a few times since the 80s is that they might be close to (or part of) Marginocephalia. In 1994, writer-researcher George Olshevsky co-opted the name Heterodontosauria (proposed in 1985 by Michael Cooper for heterodontosaurids and *Pisanosaurus* from Argentina) for a heterodontosaurid + marginocephalian clade, while a 2006 study by Xu Xing and colleagues proposed the name Heterodontosauriformes for the same group. A 2020 study by Paul-Emile Dieudonné and colleagues supported an affinity between heterodontosaurids and pachycephalosaurs, specifically finding pachycephalosaurs to be *within* heterodontosaurids. They also found the heterodontosaurids *Tianyulong* and *Echinodon* to be closer to pachycephalosaurs than are other heterodontosaurids. This would mean that heterodontosaurids are an artificial group, not a clade. At the time of writing (late 2020), the Dieudonné team's proposal awaits evaluation.

One final thing worth discussing is the role heterodontosaurids have played in discussions about dinosaur appearance. This is thanks to *Tianyulong*, a Late Jurassic, Chinese heterodontosaurid preserved with hairlike filaments and fibers. These covered at least part of the neck, body, and tail, and formed a tall mane running along the dorsal midline. Were all heterodontosaurids coated in such structures, and was the same true for other small ornithischians? And did these structures have the same evolutionary origin as the filaments of theropods and pterosaurs? Debate on this issue continues and there are competing views.

See also Marginocephalians; Ornithoscelida; Pachycephalosaurs.

Horner, Jack

An American paleontologist famous for his work on hadrosaur nesting biology, for studies of dinosaur growth and shape change, and for his role as consultant for *Jurassic Park*. Horner began his paleontological career by studying animals from well before the age of dinosaurs but is best known for his 1978 discovery of hadrosaur eggs, nesting colonies, juveniles, and adults in Montana. Horner and his colleague Bob Makela named this dinosaur *Maiasaura*. This means "good mother lizard" and refers to the evidence for parental care in this animal. These finds overhauled thinking on dinosaur behavior.

Horner and Makela didn't just find *Maiasaura* nests, but those of a smaller dinosaur too. These were initially thought to belong to the ornithopod *Orodromeus* (named by Horner and David Weishampel in 1988) but were later shown to be those of troodontid maniraptorans.

To learn more about maiasaur growth and metabolism, Horner teamed up with Armand de Ricqlès in Paris and learned how to make thin-sections of bones. This paved the way for work Horner later published on dinosaur growth strategies and also for a 2005 study—led by Mary Schweitzer—of medullary bone in *Tyrannosaurus*, a tissue previously thought unique to birds, where it functions as a calcium store used in eggshell manufacture. Some of Horner's work on growth in dinosaurs (published with Jack Scannella, Mark Goodwin, and others) proposes that ceratopsians and

pachycephalosaurs underwent *extreme ontogeny*: that is, that they underwent a surprising amount of anatomical change as they matured. In fact, Horner and his colleagues have argued that animals previously thought to be distinct taxa are actually the growth phases of others. This is controversial and other experts contest what Horner and his colleagues propose.

Horner also courted controversy during the 1990s when he argued that *Tyrannosaurus* couldn't have been an active predator but was instead a committed scavenger. This proposal—a nonstarter for ecological reasons—was refuted, most thoroughly in a 2008 article by Thomas Holtz.

Since about 2009, Horner has discussed another idea which has received substantial media coverage: namely, that improved knowledge of genetics might allow the transforming of chickens into animals resembling Mesozoic maniraptorans. This has been dubbed the "chickenosaurus" project and is apparently directly inspired by the *Jurassic World* franchise. A few relevant studies have appeared in print. These discuss how the snout, ankle, and tail bones of modern birds can be modified during early development of the embryo to resemble more archaic anatomical configurations. So far so good, but we're a long way off from seeing a living, breathing *Velociraptor*-like chickenosaur.

Thanks to his role as consultant for the *Jurassic Park* and *Jurassic World* movies, Horner has been a perpetual public figure in the dinosaur world since 1993, and his ideas and discoveries have been widely reported by the press. He's published several popular books, the best known of which are 1988's *Digging Dinosaurs*,

coauthored with James Gorman, and the 1993 *The Complete T. Rex*, coauthored with Don Lessem.

See also Hadrosaur Nesting Colonies; *Jurassic Park*.

Iguanodon

One of the three founding members of Dinosauria and only the second non-bird dinosaur to be scientifically described, *Iguanodon* is a European ornithopod famous for its spike-shaped thumb. The story of *Iguanodon*'s discovery is told in most books on dinosaurs and it seems cliché to repeat it, but here we go anyway. During the early 1820s, English paleontologist and surgeon Gideon Mantell obtained fossil teeth and bones from a rock known as the Tilgate Grit. They seemed to belong to a new kind of very large animal, but Mantell and his colleagues were unable to identify them. The Tilgate Grit was thought at the time to be geologically young, and not from that part of geological history dominated by giant reptiles.

On seeing the teeth of an iguana in 1824, Mantell realized what he had: an immense, herbivorous reptile, shaped like a gigantic iguana. He named it *Iguanodon* in 1825, though he published the name "Iguanadon" first, and it was Samuel Stutchbury who noted the iguana similarity, not Mantell. Mantell's "giant iguana" vision of *Iguanodon* was modified as more evidence came in, most notably the partial skeleton today known as the "Mantelpiece," which Mantell obtained in 1834. This specimen led Mantell to think that a nose horn might be present. His view of *Iguanodon* evolved further over the years; in 1851 (the year before he died) he argued that *Iguanodon* was bipedal, and that it perhaps had short arms.

But in 1852, Mantell's take on *Iguanodon* was overwritten by Richard Owen. Owen argued that *Iguanodon* was a short-tailed, rhino-like animal, and we know exactly what he thought thanks to the models at Crystal Palace. Fast forward to 1884, and the "true" appearance of *Iguanodon* was revealed thanks to the discovery of complete skeletons in Bernissart, Belgium. Studied by Louis Dollo and erected for display in Brussels, they showed that *Iguanodon* didn't look like Mantell's or Owen's version. Instead, it was a beaked, bird-footed animal unlike both iguanas and rhinos. The spike wasn't a nose horn but a modified thumb which seemingly served as a weapon.

Since Dollo's time, our view of *Iguanodon* has continued to change. Dollo thought it would have stood like

a kangaroo, and he had to break and dislocate the tail to get the skeletons into a kangaroo-like pose. During the 1980s, British paleontologist David Norman—working within a "post-Renaissance" paradigm in which dinosaurs were thought to walk with a horizontal body and tail—argued that *Iguanodon*'s hands were well suited for weight-bearing and that it was probably quadrupedal for most of the time. This view is supported by tracks and by studies of other iguanodontians, and the "Norman view" of what *Iguanodon* was like is now widely accepted.

In fact, Norman's studies make *Iguanodon* one of the best understood of all non-bird dinosaurs. This work was done mostly on the giant, heavily built species from Belgium (*I. bernissartensis*), which is emphatically not the same animal that Mantell brought to light in England. Mantell's "*Iguanodon*" is almost certainly not part of the same genus as *I. bernissartensis*. For that reason, it was decided in 1998 that *I. bernissartensis* should be made the name-bearing (or *type*) species for *Iguanodon*, the result being that the name *Iguanodon* is forever tied to *I. bernissartensis*. Maybe this is and was a good idea. But it's a real pain when it comes to any discussion of the history of *Iguanodon*, since it means that much of the "*Iguanodon* story" is no longer about *Iguanodon* at all.

So, what *is* the deal with the original English material which Mantell studied? In a series of papers published in 2010, Norman argued for the distinction of two English iguanodontian taxa: the heavily built *Barilium* and the more lightweight *Hypselospinus*, named for its tall vertebral spines. At least some of Mantell's material

must have belonged to either of these animals. Numerous ornithopod fossils discovered outside of England were, quite naturally, assumed to be additional *Iguanodon* species when first named back in the 1800s and early 1900s, but they are today known to have affinities that lie elsewhere.

A key part of the *Iguanodon* story as told by Gideon Mantell is that . . . well, that it was told by Gideon Mantell. Gideon's wife Mary is often mentioned in the story since she supposedly found the initial teeth while accompanying Gideon on one of his medical visits, and some researchers—most notably historian and author Dennis Dean—have argued that this part of the story is apocryphal and probably fictional. But there are reasons for thinking quite the opposite. Mary was an educated and skilled woman and produced illustrations for some of Gideon's work. They separated in 1839, Gideon eventually declared his hatred of her, and he even instructed his son Walter to remove mention of her from his journals after his death. An 1887 article, mostly overlooked prior to 2020, states that Mary found the teeth while visiting a friend and purchased them, all without Gideon's involvement. If true, this affirms her part in the story and means that she had a more important part in *Iguanodon*'s discovery than previously credited.

See also Crystal Palace; Ornithopods; Richard Owen.

Jurassic Park

A 1983 screenplay, best-selling 1990 novel, and later a film and film franchise that did more to introduce the public to the "modern view" of

dinosaurs—the Dinosaur Renaissance view—than any other effort.

Jurassic Park the screenplay and book is by American author Michael Crichton (1942–2008), best known for thrillers that involve sci-fi and future tech. Crichton's works often focus on the dangers of meddling with such things and generally have a negative view of scientific advancement. Many have been adapted into films.

Jurassic Park the novel is a cautionary tale about genetic engineering, specifically "de-extinction" when exploited for commercial ends. Dinosaurs of around 20 species are resurrected for a theme park, and right from the start it's obvious that the dinosaurs are incredibly dangerous and able to escape captivity. Chaos theory is invoked throughout the book to explain events, in particular by mathematician Ian Malcolm. Crichton obviously read Greg Paul's 1988 *Predatory Dinosaurs of the World* and some of his decisions reflect Paul's statements. He was also familiar with Jack Horner's work on hadrosaur biology, and one of the main characters—paleontologist Alan Grant—is modeled on Horner himself. So far so good, but it can also be argued that Crichton made odd decisions in his story-telling: *T. rex* has a chameleon-like tongue, many of the dinosaurs are venomous, and the dromaeosaurids have hyena-like jaw strength and are able to chew through metal bars.

Even before the novel's release, Crichton negotiated fees to turn the book into a film. Several big Hollywood names—among them Steven Spielberg, Tim Burton, and James Cameron—aimed to buy the rights, Spielberg and Universal Studios winning out. A dream-team of visionaries from the special-effects world worked to

bring the dinosaurs to life, including Phil Tippett and the people at Stan Winston Studios and Industrial Light and Magic. The innovations made in CG during the making of the movie were ground-breaking. For the first time, living, breathing animals were fully realized in CG. The effects stand up today. Several paleontological advisors were consulted. Jack Horner had the largest role, but author Don Lessem and paleontologists Mike Greenwald, Jacques Gauthier, and Rob Long also had input.

The look of *Jurassic Park*'s dinosaurs is significant in that they were about as accurate as they could be for 1993. These were dynamic, horizontal-bodied dinosaurs based on Greg Paul's skeletal reconstructions (a few of which appear in the movie), though tweaks and redesigns were made as they became adapted into characters better suited for storytelling. This especially affected *Dilophosaurus*, which became a miniature, venom-spitting animal with an erectile neck frill. The animals labeled *Velociraptor* in the film are not oversized members of that taxon but are based on *Deinonychus*; as per Crichton's novel, the film follows Paul's proposal that *Deinonychus* is a species of *Velociraptor*. Spielberg and his team also opted to keep the dinosaurs scaly. It can be argued that this was appropriate given that feathered dromaeosaurids were as yet unknown from the fossil record. And rendering feathers in CG—and applying them realistically to puppets and robots—is expensive. On the other hand, a project like this *should*—one could argue—have been daring enough to bite the bullet and feather its dinosaurs, since this always was a good, sensible idea.

Jurassic Park opened in June 1993 and saw enormous success. It grossed more than $914 million on its initial run and became the highest grossing film of all time, a record it held until *Titanic*'s success in 1997. Naturally, there were sequels: *The Lost World: Jurassic Park* in 1997 and *Jurassic Park III* in 2001, though neither are anything special. The franchise was resurrected in 2015 with *Jurassic World*, which again saw massive success. *Jurassic World* is a very different film from *Jurassic Park*, but it's deliberately similar in that it sticks with the same look for the animals. I consider this a shame given that this was otherwise an excuse to give us twenty-first-century dinosaurs instead of early 1990s ones, but, hey, movies are art, and moviemakers can tailor their vision however they like . . . or, so I'm repeatedly told whenever I've criticized the film and the look of its animals.

Jurassic Park is hailed today as being massively inspirational to many people working in paleontology. It played a crucial role in the history of western cinema and the application of digital effects and, in 2018, was recognized by the USA's Library of Congress as worthy of preservation in the United States National Film Registry.

See also Dinosaur Renaissance; Jack Horner; Greg Paul.

KPg Event

Of the several mass extinctions that have occurred throughout geological time, none is more famous than the one that put an end to the Cretaceous, 65.5 million years ago. This was the end-Cretaceous extinction event or KP or KPg Event, "KP"

and "KPg" standing for "Cretaceous and Paleogene." The geological abbreviation for Cretaceous is K because C is already in use for the Cambrian (a chunk of time extending from 541 to 485 million years ago). All dinosaur groups excepting birds disappeared during the KPg Event, as did pterosaurs, marine reptiles excepting turtles, and numerous marine invertebrate groups. Birds, lizards, mammals, and other groups had their numbers thinned by the extinction, and some studies indicate that as many as 80% of all species alive at the time disappeared. But in the public mind, the event remains synonymous with the "extinction of the dinosaurs."

For years, ideas on the KPg Event were vague and speculative, the impression created by some books and articles being that just about any idea was up for grabs. Such proposals include that mammals ate dinosaur eggs at nonsustainable rates, that caterpillars robbed herbivorous dinosaurs of leafy sustenance, that dinosaurs had simply run their course, or that it became too hot, too cold, or too seasonal. Ideas of this sort might account for the decline of one or two animal groups, but not for all the groups that died out. Experts also disagreed on the nature of the event. Some said it was sudden and devastating, others that it was drawn-out and more to do with gradual climatic and habitat change.

Nevertheless, the search for a "big cause" was often on the minds of experts. During the 1970s, discoveries in astronomy and astrophysics raised the possibility that a cataclysmic event involving a comet or supernova might have been responsible. So when, in 1980, Luis and Walter Alvarez, Frank Asaro, and Helen Michel

reported high levels of iridium in terminal Cretaceous sediments, it was immediately recognized as of great relevance. Iridium is rare on Earth and associated with extraterrestrial rocks, so here was definitive evidence for an extraterrestrial agent. The Alvarez team proposed what became known as the "Alvarez hypothesis": a large asteroid hit the Earth, disintegrated, and injected enough dust into the atmosphere to prevent photosynthesis and cause food webs to shut down.

As appealing as this idea was, it lacked support from an impact crater, since any object big enough to cause the extinction would surely have created an exceptionally large one. In fact, an impact crater of exactly the right age and size *was* known (it had been discovered during the late 1960s) but had been overlooked because it was known only to geophysicists working in the oil industry. This was the Chicxulub Crater, a 300 km-wide depression buried under the Yucatán Peninsula of Mexico. In 1991, Alan Hildebrand and a team of colleagues identified the Chicxulub Crater as the "smoking gun" that demonstrated the cause of the KPg Event. The presence of jumbled, broken Late Cretaceous rock layers, super-heated rock pellets, damaged quartz fragments, and other pieces of evidence backed up their argument that an impact had occurred on the Yucatán, 65.5 million years ago.

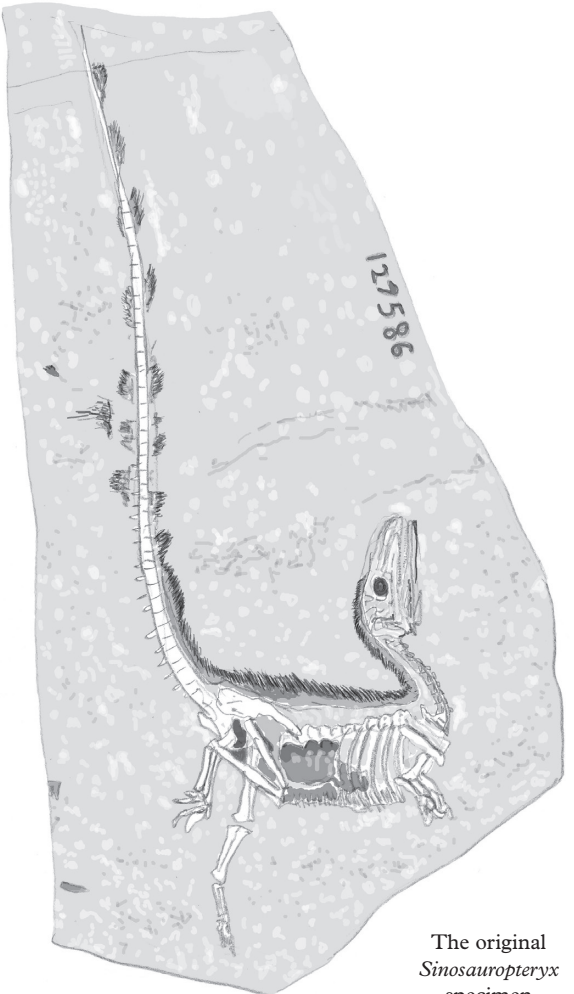
Subsequent studies have confirmed their conclusions. Claims that the crater is the wrong age, that there might be another cause of the extinction event, or that dinosaurs and other living things were in decline prior to the KPg Event have been made, but all have been falsified.

65.5 million years ago, a rock from space—between 10 and 80 km (6–50 miles) wide—collided with our planet, releasing energy equivalent to that of more than 100 million human-made nuclear bombs. Shock waves, tidal waves hundreds of meters high, and wildfires occurred immediately, and the vaporized carbonate rocks that formed the bedrock at the impact site resulted in a massive CO_2 release. Millions of living things in proximity to the impact died instantaneously, but it was the collapse of ecosystems over the next few decades that was the main cause of the extinctions that followed. It was a tragic and horrible end to an amazing period of our planet's history, but one that seems appropriately cosmic and vast, if not near unimaginable in size and scope.

Liaoning Province

Currently one of the world's most exciting and significant Mesozoic fossil locations, an area of northeast China famous for yielding thousands of feathered non-bird theropods and archaic birds in addition to numerous pterosaurs, mammals, amphibians, invertebrates and more. The name Liaoning does not pertain to a single locality but to numerous separate ones, most of which are small quarries or cliffs surrounded by farmland.

The fossil wealth of Liaoning Province became internationally famous in 1996 when the complete skeleton of a small, feathered theropod was announced via both the popular and scientific press. This was *Sinosauropteryx*, a coelurosaur closely related to Germany's *Compsognathus*. Filaments preserved across



The original
Sinosauropteryx
specimen

its body proved to be branching structures made of the same organic materials as modern feathers, and they were later shown to preserve pigment traces too. Two other feathered theropods—the vaguely birdlike *Caudipteryx* and *Protarchaeopteryx*—were announced from Liaoning in 1998, another (*Sinornithosaurus*) was published in 1999, and a fourth—the famous "four-winged" *Microraptor*—in 2000. These fossils demonstrated that John Ostrom's ideas about the dinosaurian origin of birds were correct, and also that Greg Paul and others had been correct in arguing that feathers were not unique to birds.

In the years following those early announcements, discoveries have come in so thick and fast that it's a struggle to keep up. Uncertainty about the relationships of these sediments resulted in much confusion over the age of the fossils and whether they were contemporaneous. Today we know that some Liaoning fossils—most notably those of the Tiaojishan Formation—are around 160 million years old, and thus from the Middle or Late Jurassic. The remarkable scansoriopterygids are among these Tiaojishan fossils.

A second lot of Liaoning fossils are from much younger beds (the Yixian and Jiufotang formations) that date to between 130 and 110 million years old and thus to the Early Cretaceous. Tyrannosauroids large and small are known from the Yixian and Jiufotang, as are numerous maniraptorans like oviraptorosaurs, dromaeosaurids, troodontids, and archaic birds. These are mostly small, forest-dwelling animals that lived in an area with numerous lakes and nearby volcanoes. Occasional volcanic eruptions involved both toxic gas and

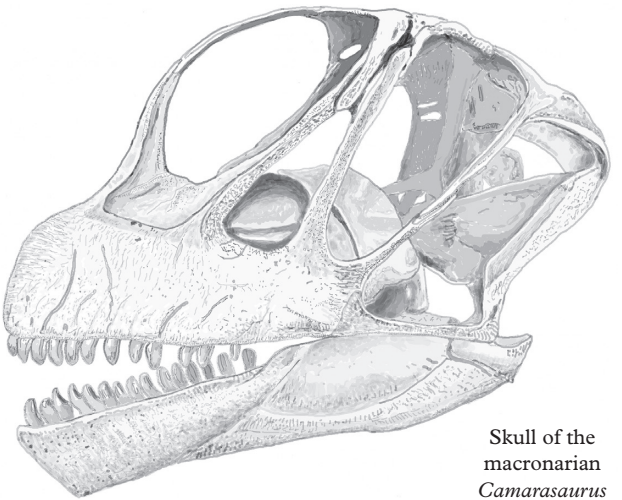
fine ash. Animals were killed and immediately buried in fine-grained sediments which prevented decay and preserved some of their soft tissues. It's not just feathers, fur, and skin, but also eyeballs and even (on occasion) internal organs like lungs that have been preserved. After decades of hoping that we'd eventually discover good numbers of the small, feathered, birdlike coelurosaurs long imagined to exist, we now have something of an embarrassment of riches.

There's one final thing worth saying about the fossils of Liaoning. The feathered Jurassic and Cretaceous dinosaurs from the region are relatively recent discoveries, but the location itself is not. In fact, Cretaceous fossils from Liaoning have been known since the 1920s. Those early finds involved arthropods and fish . . . but how might history have been different had those initial fossils included the feathered dinosaurs for which the area is famous today? We'll never know, but it's fun to imagine how different things might have been.

See also Birds; Maniraptorans; Scansoriopterygids; Tyrannosauroids.

Macronarians

The sauropod clade (properly Macronaria), which includes brachiosaurids, titanosaurs, and their close relatives. Until the early 1990s it was mostly agreed that advanced sauropods—the neosauropods—fell into two major groups. One included the slender-toothed, shallow-snouted diplodocoids and titanosaurs, and the other the spatulate-toothed, deep-snouted camarasaurs and brachiosaurids. This interpretation (which had arisen in the 1920s



Skull of the macronarian *Camarasaurus*

thanks to the work of Werner Janensch) began to fall apart around 1995 when Jorge Calvo and Leonardo Salgado in Argentina pointed out that titanosaurs had more in common with camarasaurs and brachiosaurids than with diplodocoids. By 1998—when Jeff Wilson and Paul Sereno published their landmark study of sauropod phylogeny—it was obvious that previous work had missed the existence of a major sauropod clade, one of the key features of which are gigantic nostril openings.

Wilson and Sereno named this group Macronaria, meaning "big noses." Numerous subsequent studies have backed macronarian existence. *Camarasaurus* from the Late Jurassic is one of the most archaic of macronarians and is outside the clade—Titanosauriformes—that

includes brachiosaurids and titanosaurs. The especially long-necked, east Asian euhelopodids are titanosauriforms too, as are taxa previously considered brachiosaurids but now thought more closely related to titanosaurs, like *Sauroposeidon* from the Early Cretaceous of Oklahoma.

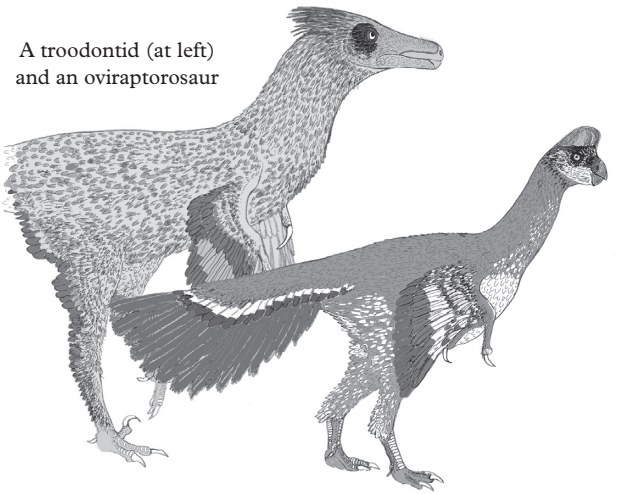
Macronarians tend to have slimmer forelimbs, longer hands, deeper bodies, and shorter tails than other sauropods, and the older clades within the group (brachiosaurids and euhelopodids among them) appear to have been specialized high-reaching browsers more so than other sauropods. However, dwarf forms evolved too, and titanosaurs evolved features absent in all other sauropods, among them bony skin plates and robust, unusually muscular limbs. A mostly unresolved question is why macronarians evolved the gigantic noses they're named for. This isn't an especially well-researched area, but it's likely their nostrils contained a high number of blood vessels and were used in dumping heat, a feature that might have given these dinosaurs an edge in the tropical environments of the low latitudes. Noise making and moisture recapture are other possible uses of the macronarian nose too.

See also Brachiosaurids; Titanosaurs.

Maniraptorans

The most successful theropod clade (if "success" is equated with species number and ecological diversity), and the only one that persists to the present. Maniraptorans—formally, Maniraptora—were named by phylogeneticist Jacques Gauthier in his classic 1986 study of dinosaur evolution.

Prior to the mid-1980s, the several maniraptoran clades were thought to have emerged independently from a coelurosaurian "central stock" that had also given rise to ornithomimosaurs and various other theropod groups. Gauthier realized that oviraptorosaurs, dromaeosaurids, and troodontids shared elongate forelimbs and reduced tails with birds, and that here was evidence for a previously overlooked clade. A crescent-shaped wrist bone termed the semilunate carpal was also shared by these groups. It allowed them to move the hands in a manner similar to that which occurs during the folding and unfolding of a bird's wing. Yet here it was in predatory animals equipped with massive hand claws. What looks likely is that the avian flight stroke had its genesis in a predatory grabbing action. The name Gauthier



A troodontid (at left) and an oviraptorosaur

chose for this clade—Maniraptora means something like "hand stealers"—refers to this fact. New fossils and much work on phylogeny has established that alvarezsaurs and therizinosaurs are also maniraptorans.

Maniraptorans were and are variable in ecology and lifestyle. The earliest members of most maniraptoran lineages were similar in size to crows or chickens, and they probably started their history as generalists, lacking specializations for any particular lifestyle. Specializations soon evolved, however. Alvarezsaurs became *really* odd, therizinosaurs and oviraptorosaurs were peculiar omnivores or herbivores, and troodontids were long-legged predators that might have indulged in some omnivory too. Birds evolved a vast number of lifestyles. When we map this variation onto a cladogram we find herbivory to be the ancestral condition for maniraptorans, which means that dromaeosaurids (the clade that includes *Velociraptor*) evolved their carnivory from herbivorous ancestors.

There's also impressive size variation within Maniraptora. Typical species were similar in size to turkeys, and quite a few were human-sized, but giants exceeding a couple of tonnes evolved among therizinosaurs and oviraptorosaurs. Giant dromaeosaurids and birds exceeding 200 kg (441 lb) also evolved. Birds of course include the smallest dinosaurs.

Spectacular fossils from China, in particular from Liaoning Province, have confirmed predictions that non-bird maniraptorans were feathered just as birds are.

See also Alvarezsaurs; Coelurosaurs; Ornithomimosaurs; Oviraptorosaurs; Scansoriopterygids; Therizinosaurs.

Marginocephalians

The so-called margin-headed ornithischians (properly Marginocephalia), a clade united by the presence of a bony shelf or margin that projects from the rear edge of the skull.

Marginocephalia itself consists of two main clades: pachycephalosaurs or boneheads, and ceratopsians or horned dinosaurs. A tendency for the skull to be specialized as a weapon and display item is obvious, though the two clades obviously went in different directions on how the skull was used. Marginocephalians tend to have a narrow beak, and early species had fang-like teeth at the front of both upper and lower jaws, too. These might have been used in aggression and foraging, and perhaps display too.

"Classic" pachycephalosaurs and ceratopsians look quite different from each other. Pachycephalosaurs are dome-skulled bipeds with short forelimbs, while ceratopsians are rhino-like quadrupeds with horns and a bony frill. For this reason, the two weren't suspected to be close relatives until it was realized that less specialized dinosaurs were part of the same story, in particular the bipedal ceratopsian *Psittacosaurus* from the Early Cretaceous of east Asia. Several studies published during the 1980s "discovered" Marginocephalia at about the same time, but only Paul Sereno opted to give the group a name. Studies also show that marginocephalians share an ancestor with ornithopods. Fossils show that ornithopods were present as early as the Middle Jurassic, so Middle Jurassic marginocephalians should be out there to find too. They've proved elusive so far, the oldest marginocephalians being Late Jurassic ceratopsians.

A long-standing controversy worth mentioning concerns the position of the heterodontosaurids. They're marginocephalian-like in some respects and might be early members of the clade. But they might not; views differ.

See also Ceratopsians; Heterodontosaurids; Pachycephalosaurs.

Megalosauroids

A mostly Jurassic tetanuran clade, named for *Megalosaurus* of Middle Jurassic England and associated mostly with Europe and North America. *Megalosaurus* was the first non-bird dinosaur to be named and scientifically described, and its remains (a partial lower jaw, part of the hip girdle, and some vertebrae and limb bones) were initially interpreted as those of a giant lizard.

These bones were discovered in a rock called the Stonesfield Slate (today, regarded as part of the Taynton Limestone Formation) in Oxfordshire, England, during the late 1700s, but not until 1824 did William Buckland scientifically describe them and award them a technical name. There's some reason for thinking that Buckland did this because he'd heard that a second giant fossil reptile—the creature named *Iguanodon* in 1825—was soon to see print. A consequence of *Megalosaurus*'s early discovery in the history of dinosaur science is that many later theropod finds—initially from Europe, but then in North America, Africa, Asia, and Australasia—were assumed to be additional species of the same genus, the result being a bloated and inaccurate view of *Megalosaurus*'s distribution and longevity that persisted into the 1980s. These supposed

"additional species of *Megalosaurus*" actually belong to far-flung sections of the theropod family tree.

Today, *Megalosaurus* is but one taxon within a group vernacularly termed the megalosauroids. This is a conservative group (though read on) of midsized and giant predators, ranging in length from about 4 to 10 m (13–33 ft). They share a long-snouted, often superficially rectangular skull, laterally compressed serrated teeth, and short but powerfully muscled forelimbs where the first and second claws were large and strongly curved. There's some suggestion that megalosauroids were longer-bodied, shorter-legged, and less birdlike in the architecture of their vertebrae and skulls than their cousins the allosauroids.

I deliberately haven't used the term "megalosaur" in this discussion, and this is because it could apply to one of three different groups. "Megalosaur" could be used for the clade Megalosauridae, the group that includes *Megalosaurus* and its closest relatives. *Torvosaurus* from the Morrison Formation and the Late Jurassic of

The megalosaurid *Torvosaurus*

Portugal and Germany is another megalosaurid, as is *Eustreptospondylus* from the English Oxford Clay. The afrovenatorines (named for *Afrovenator* from Niger) are part of Megalosauridae too. "Megalosaur" could also be used for Megalosauria, a clade that includes Megalosauridae in addition to the closely related tetanuran clade Piatnitzkysauridae (and currently unique to South America). Finally, "megalosaur" could *also* be used for the even more inclusive clade Megalosauroidea. Most studies find spinosaurids to be close kin of Megalosauria, and Megalosauroidea is the correct name for the Spinosauridae + Megalosauria clade. In an effort to remove any confusion throughout this book, I've deliberately used "megalosaurid" when referring specifically to members of Megalosauridae and "megalosauroid" when referring specifically to members of Megalosauroidea. I haven't needed to use "megalosaurian."

Right now is an especially awkward time to be writing about the relationships of these dinosaurs, since these are in flux. The 2019 description of *Asfaltovenator* from the Middle Jurassic of Argentina—a tetanuran that combines megalosauroid and allosauroid features—raises the possibility that Megalosauroidea is not a clade, and that megalosaurids and piatnitzkysaurids are closer to allosauroids than to spinosaurids. We await further studies.

One final thing worth discussing concerns spinosaurid origins. If spinosaurids really are megalosauroids, they presumably evolved from megalosaurid-like ancestors. It has occasionally been suggested that *Eustreptospondylus* is relevant to spinosaurid ancestry, an

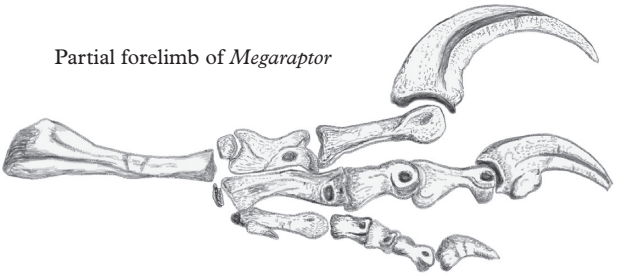
idea with some appeal given that it was found in marine rocks *and* has a skull which has been illustrated as long, low, and resembles what we'd imagine for a "proto-spinosaurid." Readers who watched the 1999 TV series *Walking With Dinosaurs* might recall *Eustreptospondylus* being shown as an island-hopping beachcomber, exactly the sort of creature that could conceivably give rise to a dynasty of crocodile-snouted fishers. But evidence is against this idea: *Eustreptospondylus* is nested within Megalosauridae and can't, then, be relevant to spinosaurid ancestry. For now, spinosaurid ancestry remains enigmatic. . . .

See also Allosauroids; Spinosaurids; Tetanurans.

Megaraptorans

A controversial tetanuran clade consisting of midsized (4–9 m [13–29.5 ft] long), mostly Gondwanan, Cretaceous taxa noted for their massive hand claws.

Megaraptorans first became known to science in 1998 when Fernando Novas described *Megaraptor* from the Late Cretaceous of Argentina. Initially, this animal was known only from a gigantic, curved claw 30 cm



Partial forelimb of *Megaraptor*

(12 in) along its curve, thought to be the sickle claw from the foot of a giant dromaeosaurid. Later finds showed that it was a hand claw from an allosauroid-like theropod with long arms. Even today the megaraptoran skeleton is poorly known, but finds from Japan and Argentina show that they possessed a long-snouted, shallow skull, relatively small teeth, a highly pneumatized skeleton, a flexible neck with ball-and-socket joints between the vertebrae, and slender legs, which indicate decent running abilities.

Several new megaraptorans have been named since 2016, including *Aoniraptor*, *Murusraptor*, and *Tratayenia*, all from Argentina. It's also been argued that a few other Argentinian theropods (originally placed elsewhere in the tetanuran tree) are members of the clade, including *Aerosteon* and *Orkoraptor*. *Australovenator* from Australia also seems to be a megaraptoran. Were they present on the Laurasian continents too? It's been said that *Eotyrannus* from the English Wealden is a megaraptoran. This is wrong since it's based on the idea that *Eotyrannus* has anatomical traits that it actually does not have.

Nevertheless, megaraptoran distribution suggests an east Asian origin during the Jurassic, since *Fukuiraptor* from Japan appears to be an archaic megaraptoran, outside the clade (termed Megaraptoridae) that contains the majority of taxa.

The great controversy about megaraptorans concerns their position in the family tree. In a 2010 study, Roger Benson and colleagues found megaraptorans to be allosauroids, and specifically part of the carcharodontosaur clade Neovenatoridae. This was an exciting claim, since

it would mean that allosauroids were a widespread and diverse clade right up to the end of the Cretaceous. It was soon challenged, though, since subsequent South American finds have led other experts to argue that megaraptorans are coelurosaurs, perhaps even members of Tyrannosauroidea. At the time of writing, the tyrannosauroid idea is looking better supported. This is also an exciting view, since it would mean that Cretaceous tyrannosauroids included an unusual assemblage of mostly Gondwanan, midsized, mega-clawed taxa in addition to the predominantly northern tyrannosaurids and their kin. The main reason for these competing views is that the anatomical features that determine where megaraptorans end up are widespread, and not unique to any specific tetanuran clade.

Essentially nothing is known about megaraptoran biology or behavior. They were clearly predatory, and presumably used those massive claws to injure and restrain their prey.

See also Allosauroids; Carcharodontosaurs; Tyrannosauroids.

Morrison Formation

A famous set of sedimentary rocks laid down during the Late Jurassic that crop out across the USA's continental western interior. The Morrison is associated in particular with Colorado and Wyoming and has produced an inordinate number of iconic dinosaur fossils.

The Morrison represents a vast chunk of sedimentary history, extending from New Mexico in the south to Canada in the north and covering around 1.5 million square kilometers, though only a fragment of this

is exposed. The sediments that form the Morrison Formation—a succession of sandstones, mudstones, siltstones, and limestones—were laid down between about 156 and 147 million years ago, during the Kimmeridgian and Tithonian stages of the Late Jurassic. The formation is named after Morrison in Colorado, the site where geologist Arthur Lakes discovered Jurassic fossils in 1877.

Familiar Morrison Formation dinosaurs include the theropods *Ceratosaurus* and *Allosaurus*, the sauropods *Camarasaurus*, *Brachiosaurus*, *Diplodocus*, and *Brontosaurus*, and the ornithischians *Stegosaurus* and *Camptosaurus*. These fossils were found mostly between 1877 and 1903 and are associated with the intense period of scientific rivalry termed the Bone Wars. Numerous small theropods and ornithischians are also known from the Morrison, as are pterosaurs, lizards, turtles, and mammals. They reveal one of the most complex, best-known ecosystems from the whole of the Mesozoic.

That statement's misleading, though, since the sediments of the Morrison don't preserve *one* ecosystem, but a great many ecosystems that can be observed changing over both time and area throughout the formation. At times, parts of the relevant region were dominated by seasonally arid, park-type environments, by swamps, lakes, and wetlands, by dense woodlands, and by deserts and hilly regions. Accordingly, you don't find the fossils of a given dinosaur throughout the whole of the Morrison; instead, it's restricted to sediments deposited in certain habitats or regions.

The association of Morrison dinosaurs with particular habitats has, in fact, proved integral to the way we've imagined dinosaurs. Between the late 1800s and

1970s, it was implied that Morrison environments were consistently humid, well vegetated, and involved lakes and rivers scattered across a massive plain. This encouraged the view that the Morrison's sauropods (and thus sauropods as a whole) were amphibious or aquatic, though it should be noted that the aquatic sauropod paradigm was—in some kind of perverse feedback loop—in part responsible for this wetland-dominated take on Morrison environments.

This interpretation was brought into question during the 1970s. Studies of Morrison sediments and their fossils showed that parts of the formation were deposited during arid conditions and on dry floodplains. This work was integral to the reinterpretation of sauropod biology that happened at the time. In fact, the two were tightly linked, since Robert Bakker and other dinosaur researchers were among those publishing this Morrison work. Since that time, a vast amount of work has been published on the fauna, flora, ecology, sedimentology, taphonomy, and geological age of the Morrison.

Those wishing for a more in-depth view of the Morrison and its fossils should seek out John Foster's substantial book *Jurassic West: The Dinosaurs of the Morrison Formation and Their World*.

See also *Brontosaurus*; Robert Bakker; Bone Wars; Sauropods.

Nanotyrannus

The name given to a kind of tyrannosaurid—mostly regarded as a growth stage of *T. rex*—originally published as a dwarf taxon that lived alongside *T. rex*. Including the name *Nanotyrannus* in this

book might be seen as a Bad Thing since it maintains belief in the idea that *Nanotyrannus* is "real" and that there's a genuine debate here.

Nanotyrannus is named for a skull discovered in the Hell Creek Formation of Montana, described by Charles Gilmore in 1946. Gilmore thought it was a new species of *Gorgosaurus* and called it *G. lancensis*. With a skull just 57 cm (22.5 in) long (yet thought to be from an adult), this animal was a dwarf compared with other tyrannosaurids. The significance of this was almost entirely overlooked. . . . until 1988, when Robert Bakker and colleagues argued that the specimen wasn't a *Gorgosaurus* at all but was instead a new kind of dwarf tyrannosaurid. They named it *Nanotyrannus*, meaning "small tyrant." Apparently, the name *Clevelanotyrannus* was considered for it at one point. Bakker and his colleagues regarded *Nanotyrannus* as similar to *T. rex* in several features, but also as highly distinct; so distinct, in fact, that it must belong to a lineage that diverged early in tyrannosaurid history. Radical stuff.

In the years following the 1988 publication of that paper, experts wavered in their acceptance of *Nanotyrannus*'s validity. The consensus view—reflected in statements made in David Weishampel, Peter Dodson, and Halszka Osmóska's 1990 *The Dinosauria*, the standard reference work on dinosaurs—was that *Nanotyrannus* (which I'll call Nano from here) was indeed a "tiny tyrant," 5.2 m (17 ft) long when alive. In a 1992 paper, however, Ken Carpenter pointed out that the features used to establish Nano's adult status were not clear-cut, and it might be a *T. rex* juvenile. This idea was taken further in a 1999 study by Thomas Carr.

Carr argued that the Nano skull was obviously that of a juvenile, and that *all* the features used to distinguish it were erroneous, or within the variation known for *T. rex*. It was no dwarf, evolutionarily distinct tyrannosaurid at all, but a juvenile *T. rex*.

Arguably, the "Nano is a juvenile" argument is more interesting than the one supporting distinct status since it shows that *T. rex* underwent a profound shift in anatomy, diet, and lifestyle as it grew, and that juveniles occupied a different niche from adults. Paleontologists have *mostly* accepted Carr's conclusions, and technical studies published in recent years have supported them. A supposed Nano dubbed Jane, discovered in 2001, possesses features that reveal it to be a *T. rex* juvenile intermediate between the original Nano specimen and noncontroversial *T. rex* specimens, and a 2020 study of internal bone structure confirmed that Nano specimens are indeed juveniles.

For all this acceptance of Carr's conclusions (it should be noted that his work is exceptionally thorough and detailed) there remains a minority who insist that Nano is its own thing. According to these researchers—Peter Larson (of Sue fame) is the most vociferous—Nano forelimbs are proportionally larger than those of *T. rex*, and the detailed anatomy of Nano's skull demonstrates distinct status. Furthermore, the existence of miniature *T. rex* teeth (similar in size to Nano teeth but with the bullet-like shape typical of adult *T. rex*) shows that the *actual* juveniles of *T. rex* were altogether different. All these points can be countered: the proportionally large Nano forelimbs are likely a juvenile feature, and the skull details are within the range of *T. rex*'s variation. As for those juvenile *T. rex* teeth, do we *really* know they're from *T. rex*? Or is it that they're from *T. rex* specimens which (while still relatively small) were more mature than the Nano specimens?

It's not *impossible* that the original *Nanotyrannus* specimen—and one, some, or all other specimens identified as *Nanotyrannus*—really is distinct from *T. rex*. But given that they're undoubtedly juveniles, they'd have to grow into something similar in size to *T. rex*; they emphatically do not belong to a dwarf taxon. Despite my vacillation, evidence showing that these animals really are juvenile *T. rex* specimens is extremely strong, and this is the conclusion we should adopt.

See also Robert Bakker; Sue; *Tyrannosaurus rex*.

Ornithischians

The major dinosaur clade, often termed "bird-hipped dinosaurs" and properly Ornithischia,

that includes thyreophorans, ornithopods, and marginocephalians. Ornithischia was coined in 1888 when Harry Seeley argued that dinosaurs could be classified into two groups, the main difference between them concerning the form of the pelvis. In one group, the pubic bones project forward and downward. Because this is the configuration seen in lizards (it is, in fact, the typical condition for reptiles and vertebrate animals in general), Seeley called this group Saurischia, meaning "lizard hipped." In another group, the pubic bones have a forward projection but are mostly directed backward and downward to extend parallel to the ischial bones. Because this configuration is seen elsewhere in birds, Seeley called this group Ornithischia, meaning "bird hipped."

Seeley also noted that saurischians had pneumatic bones while ornithischians did not. He also stated that the two groups were not closely related, and here's the beginning of the view—which was mainstream

until late in the twentieth century—that Dinosauria wasn't a clade. Indeed, Seeley's proposal was so widely adopted that you might get the impression that it was the only classification scheme put forward for dinosaurs during the 1800s, something that's far from true. Anyway, Seeley's view that dinosaurs were not a clade was eventually overturned: saurischians and ornithischians share features absent in other reptile groups.

Because the main ornithischian groups possess such distinct body shapes, the idea that Ornithischia consists of at least four subgroups was well established by the late 1800s. But views on how they might be related were vague, the general thinking maintained right up to the 1980s being that ornithopods were a "central stock" from which ankylosaurs, stegosaurs, and ceratopsians emerged. The true shape of the ornithischian family tree began to come together during the studies of the 1980s, most significantly in a 1986 study by Paul Sereno. Sereno showed that thyreophorans lack features that unite ornithopods and marginocephalians. The ornithopod + marginocephalian clade is termed Cerapoda and is part of the more inclusive clade Neornithischia.

Several major trends occurred across the course of ornithischian evolution. From small, bipedal ancestral forms they evolved increasingly complex teeth, jaws, and chewing mechanisms as well as greater size. Quadrupedality and heavyset, robust proportions evolved at least three times (in thyreophorans, iguanodontian ornithopods, and ceratopsians), and remarkably modified skulls evolved within iguanodontians and marginocephalians. However, a lightweight, cursorial body

shape and small size were retained by some lineages and persisted right to the end of the Cretaceous.

See also Marginocephalians; Ornithopods; Ornithoscelida; Saurischians; Thyreophorans.

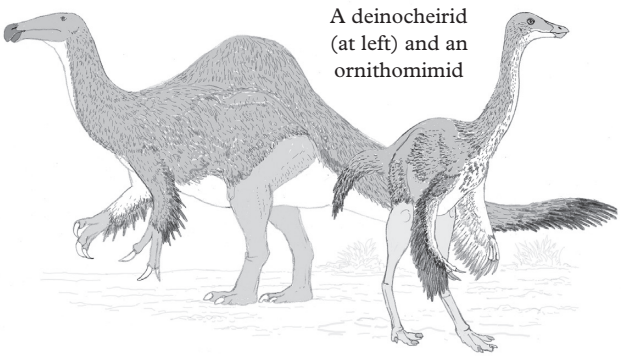
Ornithomimosaurs

Sometimes called "ostrich mimics" or "ostrich dinosaurs," a Cretaceous, mostly Asian and North American coelurosaur clade characterized by the long, slender legs, ostrich-like form, and toothless jaws of its most familiar members. The fact that ornithomimosaurs existed tens of millions of years earlier than ostriches makes it ironic that they get called "ostrich mimics" since, if anything, ostriches are ornithomimosaur mimics. But history is what it is.

Ornithomimosaurs were discovered in the 1890s when Othniel Marsh named *Ornithomimus* from the Late Cretaceous of Colorado, USA. Others—among them *Struthiomimus* and *Dromiceiomimus* from North America and *Gallimimus* and *Sinornithomimus* from Asia—were named later. It's obvious from their legs that these dinosaurs were swift runners and relied on speed when avoiding predators. Their long metatarsals (the bones between the ankle joint and toes) are locked together for strength in what's known as the arctometatarsalian condition. Associated specimens show that at least some species were social. The shapes of their jaws, their straight hand claws, and the presence of gastroliths show that they were mostly herbivorous, though it's likely that they consumed small animals on occasion. All the animals mentioned so far are very similar, the main differences between them concerning the

proportions of their hand bones. There's some variation in size, though. *Gallimimus* was a giant, sometimes 2 m (6.5 ft) at the hips and more than 8 m (26 ft) long, whereas the others were mostly 3–4 m (10–13 ft) long. All the ornithomimosaurs mentioned so far are united in Ornithomimidae; they're the ornithomimids.

Since the 1970s, many non-ornithomimid ornithomimosaurs have been named. All lack the arctometatarsalian condition. Some have teeth, ranging from a few to a remarkable 220 in *Pelecanimimus* from the Early Cretaceous of Spain. The most famous of these non-ornithomimids is the enormous *Deinocheirus* from Late Cretaceous Mongolia, named in 1972 and long known only from its arms—each 2.4 m (8 ft) long—in addition to the shoulder girdles, ribs, and some fragments. For years, this animal was an enigma, initially thought to be a megalosaurid-type animal and sometimes depicted as a long-armed super-predator. But in 1972 John Ostrom noted that it was ornithomimid-like, and the idea that it was a giant ornithomimosaur was mainstream by the



A deinocheirid (at left) and an ornithomimid

1980s. These ideas were confirmed in 2013. *Deinocheirus* was indeed a giant ornithomimosaur, but one odder than anyone had imagined. It possessed a meter-long, toothless, spoonbill-like skull, a sail, stocky hind limbs, and was about 12 m (39 ft) long and weighed more than 6 tonnes (6.6 tons). The presence of more than 1,400 small gastroliths are in keeping with a mostly herbivorous diet, but the remains of fish in its stomach suggest omnivory. Today, *Deinocheirus* and some similar, smaller taxa (*Hexing* and *Beishanlong* from China) are united within Deinocheiridae. A supposed deinocheirid from Mexico (named *Paraxenisaurus*) is of somewhat doubtful standing.

How ornithomimosaurs are related to other coelurosaurs has been the point of some uncertainty. By definition, they're outside Maniraptora, and most studies find ornithomimosaurs closer to maniraptorans than tyrannosauroids are. Alternative suggestions are that ornithomimosaurs and tyrannosauroids form a clade, or that ornithomimosaurs form a clade with therizinosaurs and alvarezsaurs.

At the time of writing, the ornithomimosaur record doesn't extend beyond the Cretaceous, even though they must have originated in the Middle Jurassic. We can say this based on the fact that the other coelurosaur groups have fossil records that extend back this far. The small *Nqwebasaurus* (it was around 1 m [3 ft] long) from the Early Cretaceous of South Africa might be an ornithomimosaur, in which case it's the oldest known.

Exceptional fossils from Canada confirm that ornithomimids—and by extension other ornithomimosaurs too—were feathered, with a shaggy pelage

covering most of the body, though not the underside or end parts of the hind limbs. Filaments or feathers projected from the arms and perhaps the hands. Was the giant *Deinocheirus* equally feathery, or did it have a sparse or reduced covering? Right now, we're not sure.

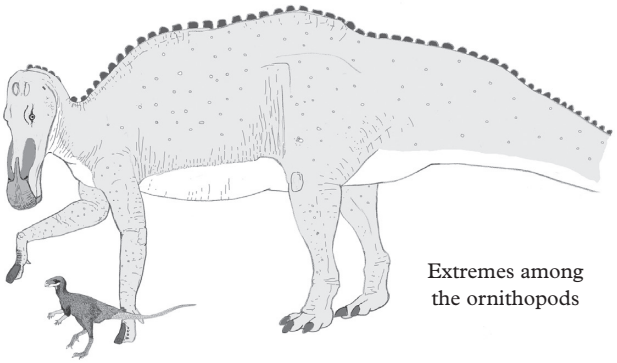
See also Coelurosaurs; Maniraptorans; Theropods.

Ornithopods

The large ornithischian clade—properly Ornithopoda—most typically thought to include the small, bipedal *Hypsilophodon* and the larger, more heavily built, quadrupedal *Iguanodon* and the hadrosaurs. In general, ornithopods were herbivores equipped with a flexible neck and lightly built forelimbs. They cropped plants with beaked upper and lower jaws and possessed complex teeth highly resistant to wear.

While the group is named for its supposedly "bird-like" feet, ornithopod feet are only superficially birdlike: they're stockier and broader than those of birds, and the first metatarsal is large and reaches the ankle in those members of the group that possess a first toe (the one equivalent to the human big toe). In the ornithopod clade Iguanodontia, the first toe and first metatarsal dwindled and disappeared. The fact that the word "ornithopod" means "bird footed" is unfortunate given that the real "bird-footed" dinosaurs are theropods, the group that includes birds themselves, but we're stuck with the burden of history and it would be unwise to disrupt convention.

The content of Ornithopoda has varied hugely over the decades. Prior to the many studies of dinosaur evolution that appeared during the 1980s, the term was



Extremes among the ornithopods

used for all those ornithischians that weren't thyreophorans or ceratopsians. During the 1980s and 90s, a few authors thought that ceratopsians should also be included within Ornithopoda and proposed that they'd evolved from *Hypsilophodon*-like animals.

But from 1986 onward (the year in which Paul Sereno published his landmark study of ornithischian phylogeny), the group's content became more precise: modern definitions link the name with the lineage that includes all taxa closer to *Iguanodon* or hadrosaurs than *Triceratops*. A range of mostly bipedal, vaguely *Hypsilophodon*-like animals—including dinosaurs traditionally grouped together as "hypsilophodontids"—are within this redefined version of Ornithopoda, a point of interest being that *Hypsilophodon* itself may not be among them. Indeed, some studies have found several "hypsilophodontid" groups (the jeholosaurids of Cretaceous China, and the parksosaurs, thescelosaurs, and orodromines of Cretaceous North America) to be

well outside Ornithopoda. The Southern Hemisphere elasmarians remain within Ornithopoda though, as do the rhabdodontomorphs and of course the "core" iguanodontians (the clade that includes *Iguanodon* and the hadrosaurs).

Evolutionary trends within Ornithopoda involve increasing size, an increase in tooth number, and an improved ability to crop and process tough plants. Hadrosaurs were not just the largest ornithopods but the ornithopods with the highest number of teeth, the most complex teeth, and the biggest, most complex beaks. However, some ornithopod lineages were conservative and might have undergone little change across their history. The rhabdodontomorphs are a possible example of this, since there are suggestions that they persisted relatively unchanged for around 100 million years.

There's abundant evidence for social behavior in iguanodontians. They mostly seem to have been herd-dwelling animals that formed nesting colonies and practiced parental care. Things are less clear when it comes to other ornithopods, though. There's evidence for parental care and group living in elasmarians, and it looks likely that at least some (perhaps most) "hypsilophodontid"-type dinosaurs lived in small herds.

See also Hadrosaurs; Heterodontosaurids; *Iguanodon*; Marginocephalians; Ornithischians; Rhabdodontomorphs.

Ornithoscelida

The proposed Ornithischia + Theropoda clade. The idea that dinosaurs could be divided into Saurischia

and Ornithischia received a hefty blow in 2017 when three British paleontologists—Matthew Baron, David Norman, and Paul Barrett—proposed an alternative model in the pages of the scientific journal *Nature*. Based on anatomical data observed in early dinosaurs discovered worldwide, they argued that the conventional family tree was wrong, and that theropods and ornithischians should be united in a clade that excludes sauropodomorphs and herrerasaurs. In contrast to most high-profile scientific claims, this discovery was kept quiet right up to publication, so it exploded on the scene as a bit of a bombshell.

The name "Ornithoscelida" wasn't new but had been proposed by "Darwin's bulldog" Thomas Huxley in 1870. Huxley proposed the name for a group that included both the Jurassic coelurosaur *Compsognathus* (regarded by Huxley as representing the new group Compsognatha) and Dinosauria, understood by Huxley to include Megalosauridae, Scelidosauridae, and Iguanodontidae. The Baron team's use of Ornithoscelida has made people think that Huxley's use of that term excluded sauropodomorphs. But it didn't, since he included the sauropod *Cetiosaurus* within Dinosauria (specifically, within his version of Iguanodontidae). The Baron team's usage of Ornithoscelida isn't, therefore, in keeping with the term's original use.

Whatever, their proposal meant that Saurischia of tradition was no more (they opted—unwisely, I think—to retain the name for the herrerasaur + sauropodomorph clade). Based on the anatomy of the earliest ornithischians, theropods and sauropodomorphs, they posited an omnivorous mode of life for the dinosaur common

ancestor, in which case the predatory habits of herrerasaurs and advanced theropods would have to be convergent. And because of the positions they found for near-dinosaurs like *Saltopus* and *Agnosphitys* (both of which are from the UK), they suggested that dinosaurs might have originated in the north, not in the south as otherwise agreed.

Studies challenging this proposal swiftly appeared: just about everyone academically interested in dinosaur evolution wanted a piece of the action. One study found Phytodinosauria supported in some iterations of the data, and a follow-up paper by Matt Baron even proposed that Ornithischia might be nested *within* Theropoda.

At the time of writing, opinion is divided on how right the Ornithoscelida model might be. Some experts think that the evidence marshaled in support of ornithoscelidan existence is bogus and due to error and imprecise interpretation of the anatomical details. Others think that there's support for its reality and that—while mistakes have been made—there's still a good indication from the distribution of anatomical features that it's legit. And yet others are on the fence and think that the real answer might be intractable. That last possibility seems like a cop-out, but we've learned from molecular phylogenetics that the evolutionary radiations of some groups were so rapid and explosive, and involved so much hybridization and gene-swapping between populations, that their pattern of evolution was star-shaped. So maybe time will tell, but maybe it won't.

See also Ornithischia; Phytodinosauria; Saurischia.

Osmólska, Halszka

A Polish fossil hunter and paleontologist (1930–2008), best known for her work on Late Cretaceous Mongolian theropods, hadrosaurs, pachycephalosaurs, and ceratopsians. Despite being best known as a dinosaur worker, Osmólska began her academic career as a trilobite specialist. A change in the direction of her career was initiated in 1963 when she joined the Polish-Mongolian Paleontological Expeditions to the Gobi Desert and began to study dinosaurs, though whether she was interested in them beforehand isn't recorded, and she was still working on trilobites in the early 1970s.

Osmólska's first dinosaur-themed publication, coauthored with Ewa Roniewicz and published in 1970, was on the ornithomimosaur *Deinocheirus*, an enigmatic and fascinating dinosaur that soon became a "superstar" of the dinosaur literature. Indeed, Osmólska's list of dinosaur publications reads like a who's who of Mongolian Cretaceous superstar dinosaurs and involves anatomical studies of ornithomimosaur, dromaeosaurid, troodontid, and oviraptorosaur species. She also published on ornithischian skull anatomy and, with Teresa Maryańska, on Asian hadrosaurs and pachycephalosaurs. In a 2002 paper coauthored with Maryańska and Mieczysław Wolsan, she argued that oviraptorosaurs should be included within the bird clade. This bold claim could be seen as providing support for Greg Paul's idea that some Mesozoic maniraptorans were the flightless descendants of *Archaeopteryx*-like animals, though in this case the results seem to be an error caused by the inclusion of too few birds in the study. With David Weishampel and Peter Dodson, Osmólska

coedited the great standard reference work on Mesozoic dinosaurs, 1990's *The Dinosauria*.

An indication of the esteem with which Osmólska was and is held comes from the fact that she's commemorated in the names of the oviraptorosaur *Citipati osmolskae*, the dromaeosaurids *Velociraptor osmolskae* and *Halszkaraptor*, the Triassic reptile *Osmolskina*, and the fossil rabbit *Prolagus osmolskae*. An obituary written by Magdalena Borsuk-Białynicka described Osmólska as a "helpful and unselfish advisor" and a "gentle, serene and wise colleague."

See also Greg Paul; Maniraptorans; Ornithomimosaurs; Oviraptorosaurs.

Ostrom, John

The paleontologist most responsible—together with his student Robert Bakker—for kick-starting scientific interest in dinosaurs. Ostrom (1928–2005) was based at the Peabody Museum of Natural History at Yale University and was highly active in dinosaur studies between the early 1960s and late 90s. He published on hadrosaurs, on the chewing mechanics of ceratopsians, and on social behavior and endothermy in dinosaurs generally. He also described and reinterpreted *Compsognathus* and *Triceratops*. Ostrom was also a teacher and academic supervisor in charge of PhD students.

Ostrom is, however, best known for his foundational studies on bird origins. These involved the anatomy and lifestyle of maniraptorans (in particular *Deinonychus* and *Archaeopteryx*), and the origin and evolution of the avian flapping stroke. Virtually everything happening

in Mesozoic maniraptoran studies today can be traced back to these works.

Two independent lines of inquiry set Ostrom on the path to studying these things. During the late 1960s, Ostrom planned to study pterosaurs. He visited Europe to see fossils from the Jurassic Solnhofen Limestone. While studying a specimen at the Teylers Museum in Haarlem, the Netherlands, he realized it wasn't a pterosaur at all: it was a theropod, specifically an *Archaeopteryx* (though read on). This was a big deal in scientific terms (Ostrom got a *Science* paper out of it), but it was also a big deal for Ostrom personally, since it inspired him to study *Archaeopteryx* in depth. Coincident with these studies was his work on a theropod discovered in 1964: *Deinonychus*, which Ostrom named and described in 1969. This agile, dynamic dinosaur—Ostrom described how it would have used its rodlike tail in balancing and switchblade-like toe claws to disembowel prey—caused a sensation. In a 1978 *National Geographic* article, Ostrom showcased *Deinonychus* and other new discoveries and promoted a new view of dinosaurs. This was all part of what Bakker termed the Dinosaur Renaissance.

The detailed anatomy of *Deinonychus* was strikingly similar to that of *Archaeopteryx*, and here's where Ostrom's two strands of research came together. *Deinonychus* wasn't a bird ancestor (it lived well after animals like *Archaeopteryx*), but it seemingly showed what bird ancestors were like, and how they lived and functioned. Throughout the 1970s and 80s, Ostrom argued that birds evolved from *Deinonychus*-like theropods, his main argument being that the flapping stroke evolved in

a terrestrial setting from theropods that used a grabbing motion when capturing prey. This was a "ground-up" model of flight, and it couched *Archaeopteryx* as a ground dweller.

Subsequent work and discoveries, especially those published during the 1980s, led to widespread acceptance of Ostrom's proposals. He became increasingly respected as prescient and broadly correct, but also appropriately conservative and nuanced in his conclusions and rigorous in his analyses. The 1984 International *Archaeopteryx* Conference, held in Eichstätt, Germany, made it clear that Ostrom's views on bird origins were *the* talking point of the entire field, and it was also clear by this time that his views had instigated a paradigm shift.

The announcement of the feathered Liaoning Province coelurosaur *Sinosauropteryx* in 1996—hailed at the time as the "first feathered dinosaur" (sans birds)—was regarded by Ostrom as vindication for his views, and it's fitting that he learned of the feathered fossils of Liaoning during the last years of his life. He died in 2005 from complications linked to Alzheimer's disease. Some indication of the prestige with which Ostrom is remembered come from the fact that four dinosaurs—*Utahraptor ostrommaysi*, *Rahonavis ostromi*, *Bagaraatan ostromi*, and *Ostromia*—have been named in his honor. The Haarlem "*Archaeopteryx*" that Ostrom reidentified in 1970 turned out to be a new maniraptoran taxon, named *Ostromia* in 2017.

See also *Archaeopteryx*; Robert Bakker; *Deinonychus*; Dinosaur Renaissance; Liaoning Province; Maniraptorans.

Oviraptorosaurs

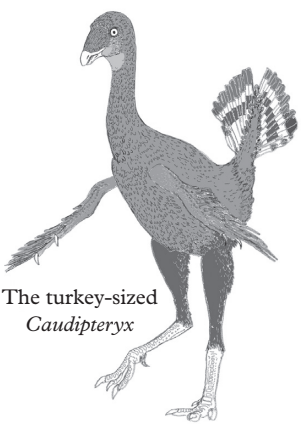
A mostly Asian and North American maniraptoran clade notable for their short-snouted, often crested, and toothless skulls as well as for the association of some taxa with eggs and nests. Oviraptorosaurs—technically, Oviraptorosauria—are named for *Oviraptor* from Late Cretaceous Mongolia, a human-sized theropod discovered on a 1923 American Museum of Natural History expedition. Because it was discovered in association with an egg-filled nest—and was unusual in skull anatomy to boot—it was interpreted as an egg predator which had been discovered "caught in the act" of plundering the nest of the ceratopsian *Protoceratops*. This explains its name: *Oviraptor* means "egg thief." But the 1995 discovery of an oviraptorosaur preserved on top of a nest filled with "*Protoceratops*" eggs proved that the 1923 specimen wasn't thieving eggs at all. It was looking after its own.

Oviraptor is part of an oviraptorosaurian group (Oviraptoridae) that includes around 20 deep-faced, short-jawed Asian taxa. A second subgroup—Caenagnathidae—includes Asian and North American taxa, many of which have longer, shallower jaws and longer, slimmer limbs than oviraptorids. The namesake member of Caenagnathidae—*Caenagnathus* from Alberta, named in 1940—was initially known from a lower jaw thought to be from a giant flightless bird, meaning that there was a time when people imagined ostrich-like animals to share the landscape with *Triceratops* and *T. rex*. About 15 caenagnathid taxa are presently known. The smallest were turkey-sized, others were a more respectable 2–4 m (6.5–13 ft) long, but the enormous

Gigantoraptor from China was 8 m (26 ft) long and weighed 2 tonnes (2.2 tons). *Gigantoraptor* isn't definitely a caenagnathid but, whatever, it's the biggest oviraptorosaur and one of the biggest of all maniraptorans.

Proportionally short, robust tails are typical of oviraptorosaurs, and the vertebrae at the tail tip are fused together in some species. Caenagnathids have specialized feet where the metatarsals (the long bones in between the ankle and the toes) are locked together for strength. Some have an unusual version of this condition where the metatarsals are fused together at the ankle end.

A few other oviraptorosaur groups are outside the clade that contains oviraptorids and caenagnathids. There are the avimimids—a small, Asian and Canadian group of turkey-sized animals notable for having small forelimbs and caenagnathid-like, partially fused metatarsals—and the Early Cretaceous, Chinese caudipterids. These have teeth. The namesake member of this group—*Caudipteryx* from Liaoning—is preserved with intact feathering (most obviously, long forelimb feathers and a fanlike tail arrangement). It caused a sensation when published, since it was the first non-bird dinosaur indisputably preserved with complex feathers. *Protarchaeopteryx*, described in



The turkey-sized *Caudipteryx*

the same 1998 paper and also preserving feathers, is a toothed oviraptorosaur too, but its affinities are unclear.

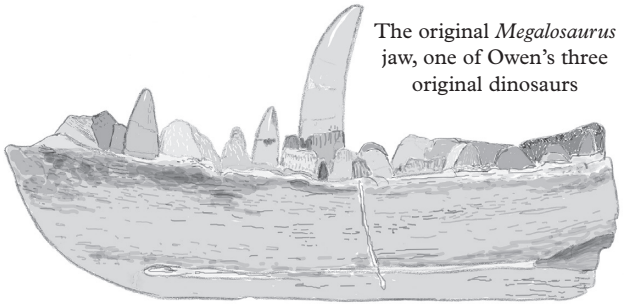
How did oviraptorosaurs live? Their jaw and skull shapes have led some to regard them as predators of molluscs or small vertebrates, or as herbivores. Stomach stones (properly termed gastroliths) show that *Caudipteryx* was mostly herbivorous, and herbivory looks likely for the group in general. But this by no means excludes the possibility that they grabbed and ate small animals when opportunity arose. Aggregations show that some species lived in groups, and there are even specimens preserved huddled together in sleeping poses. The muscular tails of these dinosaurs have led to suggestions that they used their fanlike tail-feather arrangements in peacock-like fashion, most likely in courtship displays.

A final thing worth considering is how oviraptorosaurs relate to other maniraptoran clades. The idea mostly favored today is that oviraptorosaurs are close relatives of dromaeosaurids, troodontids, and birds, and that all four groups form a clade termed Pennaraptora. However, it's been suggested on occasion that oviraptorosaurs might form a clade with therizinosaurs. Both have similar neck vertebrae, and there are similarities in their claws and hips.

See also Maniraptorans; Therizinosaurs.

Owen, Richard

One of the most accomplished and experienced anatomists, paleontologists, and zoologists of the Victorian Era. Richard Owen (1804–1892)—he became *Sir* Richard in 1883—is famously associated with dinosaurs



The original *Megalosaurus* jaw, one of Owen's three original dinosaurs

because he coined the word Dinosauria itself in his 1842 report on British fossil reptiles. In that work, he described how three recently named fossil reptiles from England—*Megalosaurus*, *Iguanodon*, and *Hylaeosaurus*—were united by a high number of sacral vertebrae, massive limb bones, and features of the vertebrae and ribs.

Owen regarded these animals as reptilian versions of rhinos and elephants—as "pachydermal" reptiles—and his views on their appearance is immortalized at Crystal Palace. Science historian Adrian Desmond argued that Owen's view of dinosaurs as pachydermal was partly a response to the evolutionary views that were becoming popular at the time: he deliberately used dinosaurs to show that life hadn't necessarily "improved" over time, since dinosaurs—gigantic, pachyderm-like reptiles—could obviously not be regarded as the lowly ancestors of today's small, creeping lizards and snakes. Owen also described *Cetiosaurus* in 1841. This was the first sauropod to be scientifically described, but Owen didn't know it was a dinosaur and regarded it as a massive sea-going relative of crocodiles. His 1863 description

of the thyreophoran *Scelidosaurus* is also significant in being the first study of a complete, articulated Mesozoic dinosaur skeleton.

For all his fame as a describer of fossil reptiles, Owen was originally an anatomist. He trained in medicine at the University of Edinburgh in Scotland before switching to scientific research while at the Royal College of Surgeons in London. His aim was to become the "British Cuvier," an informal title coveted by those in British biological science at the time. He became superintendent of the natural history department of the British Museum in 1856, and in 1859 proposed the construction of a dedicated, London-based natural history museum. This "cathedral to nature" opened in 1882 and was a radical new vision of what museums should be. It remains a world-famous center of research and exhibition today, strongly associated with dinosaurs due to its exhibits, collections, and the research of its staff.

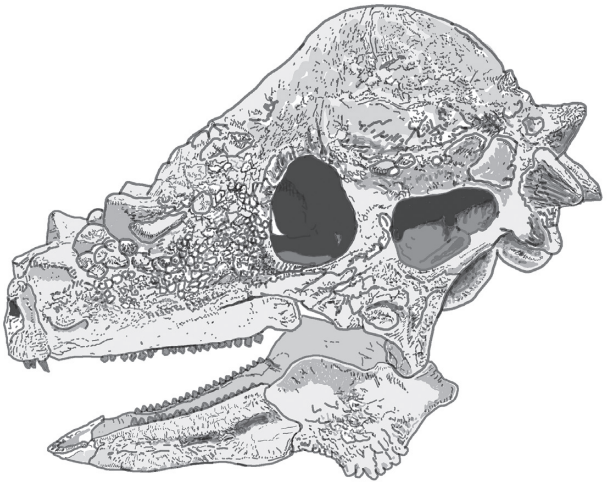
Owen's familiarity with animals of all sorts, fossils and living, led him to propose numerous ideas on the history of life and on how new forms were generated. He opposed Darwin's model of evolution by natural selection and was also, on regular occasion, unpleasant to colleagues and contemporaries. He battled with Gideon Mantell, and Thomas Huxley wrote how he was "feared and hated." For these reasons, Owen is frequently framed as a villain in the history of paleontology and zoology. While he was no saint, much of this is unfair and inaccurate. It fails to account for his vast contributions to science and for his ability to keep biology and paleontology in the public eye.

See also Crystal Palace.

Pachycephalosaurs
Also known as boneheads or dome-skulled dinosaurs, a mostly Late Cretaceous Asian and North American bipedal ornithischian clade famous for their thick-boned skulls. Taxa range from 1 to 5 m (1–16 ft) in length. Small, vaguely leaf-shaped teeth show that they were leaf eaters. There are also caniniform teeth at the front of the mouth that were perhaps used in fighting, or in biting fruit or small animals. These teeth are superficially similar to those of troodontid maniraptorans, and a consequence is that both groups were considered one and the same for more than 40 years.

The pachycephalosaur skeleton is poorly known, and we're waiting for discoveries to shed light on many aspects of their anatomy. We know that the arms and hands are small, that the hips and tailbase are wide, and that bony rods were embedded in the musculature of the tail. These rods were originally thought to be ossified tendons like those connected to the vertebrae of other ornithischians. They're actually intermuscular bones, structures seen elsewhere in ray-finned fish. They might show that the tail was chunky and perhaps used as a fat store, a weapon, or even a prop.

For a while, pachycephalosaurs were thought to fall into two groups: flat-skulled homalocephalids and dome-skulled pachycephalosaurids. The founding member of the homalocephalid group—*Homalocephale* from Mongolia—is similar to the contemporary pachycephalosaurid *Prenocephale*, the main difference being that *Prenocephale* has a domed skull.



Perhaps *Prenocephale* is the adult form, and the dome only appeared at maturity. This idea has been applied to North American pachycephalosaurs as well as Asian ones, but a problem is that the American animals—namely *Dracorex* and *Stygimoloch*—are elaborate, with spikes and hornlets not seen in their supposed adult form (*Pachycephalosaurus*). If these really are part of the same growth series, profound growth changes—*extreme ontogeny*—occurred as they matured.

The thick pachycephalosaur skull has led to the idea that they behaved like sheep or goats, smashing their heads together when fighting for dominance or access to mates. The fact that the majority of pachycephalosaur specimens consist of partial, worn domes—seemingly transported some distance from upland

environments—also led to the suggestion that these were animals of mountainous places. Subsequent study has called these ideas into question. Pachycephalosaur skulls aren't built for high-speed collision but instead for shoving or side-to-side butting, and studies of pachycephalosaur occurrence show that their remains are frequently preserved in lowland settings, so there's no reason to think of them as animals of the uplands.

Finally, how are pachycephalosaurs related to other ornithischians? During the late twentieth century, the bipedal body shape and lack of body armor in pachycephalosaurs meant they were regarded as ornithopods and imagined to descend from *Hypsilophodon*-like animals. In 1974, Teresa Maryańska and Halszka Osmólska argued that this was incorrect. They thought that pachycephalosaurs were a distinct group that warranted their own "suborder." As studies on dinosaur phylogeny continued during the 1980s, several authors drew attention to features shared by pachycephalosaurs and ceratopsians. A few initial proposals placed pachycephalosaurs, ceratopsians, stegosaurs, and ankylosaurs together (you can see this promoted in Robert Bakker's *Dinosaur Heresies* of 1986). But it eventually became obvious that ankylosaurs and stegosaurs (united in Thyreophora) were outside the clade that contains all other ornithischians, that ornithopods were close kin of pachycephalosaurs and ceratopsians, and that pachycephalosaurs and ceratopsians formed a clade. This was dubbed Marginocephalia in Paul Sereno's landmark 1986 study of ornithischian phylogeny.

See also Marginocephalians; Ornithischians.

Paul, Greg

A US-based paleoartist and researcher, heavily responsible for the modern look of non-bird dinosaurs and among the world's most influential illustrators of ancient life.

Paul counts among his inspirations Charles Knight, Bill Berry, and Jay Matternes, but it was his discovery of Robert Bakker's work in the early 1970s that made him aware of the Dinosaur Renaissance. Thereafter, Paul studied informally under Bakker at Johns Hopkins University in Baltimore and began producing artwork of a professional standard. Significant among his contentions (published from the early 80s onward) were that small theropods should be reconstructed with feathers, that sauropods were complex in form (not shapeless and lumpen as artists had tended to show), and that dromaeosaurids and other maniraptorans were probably the flightless descendants of flight-capable, *Archaeopteryx*-like animals.

The first public outings of Paul's illustrations were in *Science* and *Natural History* (where they accompanied articles by Stephen Jay Gould) during the late 70s. By the late 80s he was a major force in the paleoart world. Numerous of his pieces appeared in the traveling *Dinosaurs Past and Present* exhibition of 1986–91, and his article in the accompanying volume—titled "The science and art of restoring the life appearance of dinosaurs and their relatives—a rigorous how-to guide"—remains widely consulted. Paul's style of showing skeletal reconstructions (they depict the animal in a running pose, a black soft tissue outline surrounding the bones)

has been widely adopted, and his high-fidelity, ultra-detailed life reconstructions have a unique look that few have successfully copied.

Various of Paul's contentions about dinosaurs appeared in technical articles published from 1984 onward, but they're mostly remembered for appearing in his 1988 *Predatory Dinosaurs of the World* (*PDW* for short). *PDW* had its detractors and was criticized by several paleontologists shortly after publication. They decried Paul's confident pronouncements about dinosaur behavior, his promotion of dinosaurian endothermy, and his take on phylogeny and taxonomy. *PDW*'s foreword explains how it was intended to be the first in a series that would review the fossil archosaurs of the world, but both this negative response, and the changing world of publishing, meant that such plans were ultimately abandoned.

Such is the interest in Paul's work that there has long been call for a book devoted to his skeletal reconstructions and artworks. This was realized in 1996 with *The Complete Illustrated Guide to Dinosaur Skeletons*, but the fact that it was available only in Japan limited its availability. The 2010 appearance of the more comprehensive *The Princeton Field Guide to Dinosaurs* (titled *Dinosaurs: A Field Guide* in the UK) solved this problem. For many interested parties, this work is the go-to guide on dinosaur reconstructions. At the time of writing, Greg continues to occasionally publish both technical papers and books.

I've been saying the same thing about Greg Paul for years: I get the feeling from some academics that Paul is regarded as "just an artist" with avant-garde

opinions and irrelevant to proper paleontological work. What this misses is that it's specifically *Greg Paul's* vision of dinosaurs that has galvanized and inspired a great many people to study dinosaurs, or be attracted to them as objects of interest. These things are certainly true of paleoartists, but they're true of a great many scientists too. And if you were inspired by the dinosaurs of *Jurassic Park* (and its follow-up films), this includes you too, since it's Paul's reconstructions that were integral to the dinosaurs of that movie.

See also Robert Bakker; Dinosaur Renaissance.

Phytodinosauria

A proposed clade that incorporates ornithischians and sauropodomorphs. The decades since the Dinosaur Renaissance have mostly seen continuing refinement and bolstering of the idea that Dinosauria is divided into Saurischia and Ornithischia. This is familiar stuff repeated in every book on dinosaurs. Less well known is that an alternative classification was put forward during the 1980s. It proposed that Saurischia was artificial, and that sauropodomorphs and ornithischians should be united in Phytodinosauria, a name meaning "plant dinosaurs."

This concept was put forward by Robert Bakker in his 1986 *The Dinosaur Heresies*. Bakker thought that ornithischians descended from sauropodomorphs like *Anchisaurus*, and he drew attention to shared features of the jaw joint, chest bones, and thumb. Independently, Michael Cooper in South Africa also found support for a sauropodomorph + ornithischian clade that he termed Ornithischiformes.

Bakker didn't expand on his phytodinosaur proposal, but it was adopted by paleoartist (and Bakkerian protégé) Greg Paul. Writer-researcher George Olshevsky also promoted phytodinosaurian monophyly in his articles. Paul voiced support for Phytodinosauria in his 1988 book *Predatory Dinosaurs of the World* and also in a 1984 paper . . . which leads us to a curious tangent, since Paul's paper was about therizinosaurs. Paul's conclusion was that therizinosaurs were "intermediate between prosauropods and ornithischians," but this only makes sense if prosauropods and ornithischians form a clade that doesn't include theropods. Paul's conclusions were therefore contingent on the existence of Phytodinosauria, even though this wasn't stated in the paper. But the mid-80s were also the time at which the Saurischia/Ornithischia model of dinosaur phylogeny was becoming firmed up, the result being that the recognition of Phytodinosauria (and the inclusion of therizinosaurs within it) was untenable. And thus Phytodinosauria became forgotten. . . .

Until 2017. As a consequence of the Ornithoscelida debate, a number of authors analyzed dinosaur relations anew, and at least some trees recovered in these studies reveal a Phytodinosauria. While this result doesn't appear accurate, the fact is that the term Phytodinosauria is once more present in the literature.

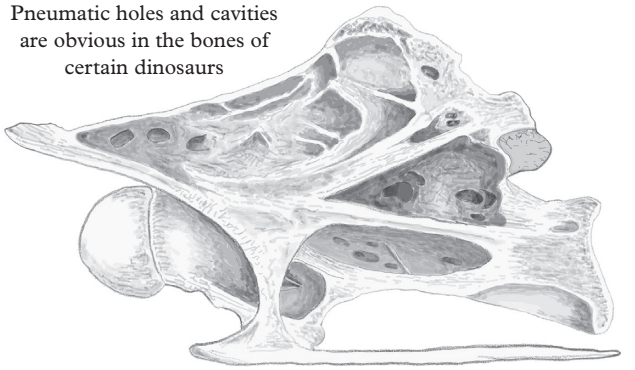
See also Robert Bakker; Greg Paul; Ornithischia; Ornithoscelida; Saurischia; Therizinosaurs.

Pneumaticity

The condition of possessing air-filled structures termed air sacs which are connected, via tubes, to the lungs and

to other parts of the pneumatic system. Pneumaticity is typical of parts of the mammalian skull, but it's especially prominent in birds where some, most, or even all of the skeleton is air-filled. In birds, additional air sacs are also present throughout the body cavity. There are typically three air sac pairs located in the chest and abdomen, while an additional sac is at the front of the chest. Because everything in the pneumatic system is connected, air moves throughout the entire system every time a breath is taken: it doesn't just move in and out of the lungs. To be clear, pneumaticity can pertain to the presence of air-filled structures in the skeleton alone, in the body cavity alone, or in both.

Bony clues demonstrate the presence of pneumaticity in extinct dinosaurs. On the outside of pneumatic vertebrae, there are large hollows called pneumatic fossae and smaller openings termed pneumatic foramina, and on the inside of these bones there are both large (camerae) and small (camellae) chambers. Thanks to



Pneumatic holes and cavities are obvious in the bones of certain dinosaurs

these features, we know that sauropodomorphs and non-bird theropods were pneumatic, this being one of several features encouraging the view that they should be united within Saurischia. Bigger species tend to be more pneumatic than small ones: giant sauropods and theropods are among the most pneumatic animals of all.

Convincing cases of pneumaticity have yet to be reported in any ornithischian, though it remains possible that they possessed air sacs in the body cavity and not in the skeleton. Outside of Dinosauria, pterosaurs are pneumatic, as are some Triassic members of the crocodylian lineage. This could mean that those archosaurs ancestral to dinosaurs were pneumatic (in which case ornithischians lost skeletal pneumaticity), or it could be that it evolved two or more times independently, we're not sure.

Pneumaticity likely provides several advantages to those animals that have it. The presence of air sacs in the body cavity allows those animals that have them to inspire more air than would otherwise be the case, so it probably makes them better at extracting oxygen from the atmosphere. Perhaps this gave dinosaurs and other archosaurs an advantage in the low-oxygen conditions of the early Mesozoic. Filling up bones and body space with air-filled cavities is also advantageous, especially for big animals, as it reduces weight.

Prosauropods

An older name, essentially used for all sauropodomorphs that are not sauropods. The concept of a "Prosauropoda" arose between 1920 and 1956 in the works of German paleontologist Friedrich von Huene. Huene

proposed that several Triassic and Early Jurassic dinosaurs should be united in a group that was related to, but distinct from, sauropods and so-called carnosaurian theropods.

The core member of Huene's Prosauropoda was *Plateosaurus* from Late Triassic western Europe. It's around 8 m (26 ft) long, long-necked, and has serrated, leaf-shaped teeth as well as fanglike teeth at the fronts of its jaws. This is a dentition suited mostly for plant-eating yet suggesting the occasional consumption of animals or carrion. It might be that most of these dinosaurs were omnivores, able to make a living in all kinds of environments and on all sorts of foods.

The big hands and strong arms of *Plateosaurus* and its kin have led some experts to regard these animals as

Plateosaurus

quadrupeds. But articulated skeletons show that their palms faced inward, not downward, and computer modeling confirms that they were bipeds. Their big hand claws (the thumb claw was especially big) were probably used in fighting and self-defense.

Tracks and skeletons preserved in close proximity show that some prosauropods were herd dwellers. Fossil eggs and babies found in Argentina and South Africa show that some underwent major changes in appearance as they grew, perhaps switching from quadrupedality to bipedality. The fact that adults have been found close to nests might mean that these dinosaurs practiced parental care. *Plateosaurus* juveniles were not that different in their proportions from adults, however, so it might be that variable strategies were used within the group. On that note, there's evidence from bone structure that *Plateosaurus* had a variable growth rate. Some individuals stopped growing at 5 m (16 ft) when they were 12 years old, while others were still growing, albeit slowly, in their third decade and after exceeding 8 m (26 ft). Maybe this variability was linked to different environmental conditions.

By the late twentieth century, experts mostly agreed that the oldest prosauropods were Triassic dinosaurs like *Thecodontosaurus* from the UK, a bipedal herbivore or omnivore about 2 m (6.5 ft) long. Animals like this were thought to have given rise to the larger, longer-necked *Anchisaurus* from the USA and *Massospondylus* from southern Africa—both of the Early Jurassic—as well as to *Plateosaurus*. And *Plateosaurus*-type animals were evidently close to the ancestry of the melanorosaurids, a group of enormous, quadrupedal, sauropod-like

herbivores, some of which were more than 10 m (33 ft) long. Because melanorosaurids are sauropod-like, some experts regarded them as the direct ancestors of sauropods. A view popular between the 1960s and 90s, however, is that they weren't sauropod ancestors at all, and in fact that prosauropods and sauropods shared an ancestor which must have been a *Thecodontosaurus*-like, Triassic dinosaur.

Today, the view that there's a clade corresponding to von Huene's concept of Prosauropoda has fallen away. Instead, it seems that these animals form a series of lineages that are successively closer to Sauropoda. *Thecodontosaurus* is among the furthest away, while the melanorosaurids are very close to Sauropoda. The fact that the lineages concerned don't group together explains why the term "prosauropod" has mostly fallen out of fashion. The preferred term for the lineages concerned is currently "non-sauropod sauropodomorph" . . . which is less euphonious for sure.

See also Sauropodomorphs.

Raptor Prey Restraint (or RPR)

The predation style suggested for predatory maniraptorans, in particular dromaeosaurids, the group that includes *Deinonychus* and *Velociraptor*. This model—inspired by and similar to the so-called mantling behavior of hawks, eagles, and falcons—involves the subduing of a prey animal by standing on top of it while pinning it down with large, strongly curved foot claws. It was published in 2011 by Denver Fowler and colleagues following their studies of predation in living birds of prey.

Previously mostly unappreciated is that these birds are like dromaeosaurids in having an especially big, strongly curved claw on the second toe. In dromaeosaurids this claw is often called the "sickle claw." After seizing a prey item, the bird uses its weight to pin the animal to the ground. The big second toe claw is latched on to the animal to maintain a grip and prevent escape. With the prey immobilized, the predator begins feeding, the prey frequently being consumed while very much still alive.

Fowler and colleagues named this predation style Raptor Prey Restraint, or RPR, and the idea that dromaeosaurids (albeit not all of them!) were specialized for RPR is appealing. The large, fully feathered forelimbs and long, fully feathered tail could have been used to help the animal maintain balance on top of a struggling prey item. Use of the technique also seems consistent with the flexible, sharp-clawed feet of these dinosaurs, the relatively short, stocky metatarsal section

of the foot (which would have helped the predator transfer its weight to the prey), and with the fact that the sickle claw appears best suited for pinning or gripping prey smaller than the predator.

This idea replaces older ideas about dromaeosaurid predation where the sickle claw was imagined as a slicing or tearing weapon, used to open the prey's flank or belly such that it might be disemboweled or bleed to death. Such ideas were put forward by John Ostrom in his studies of *Deinonychus*, but they don't really work, since sickle claws weren't shaped to cut or slice things. This was demonstrated in a 2006 study that used a robotic limb and replica claw.

Fowler and colleagues suggested that their acronym for this predation style—RPR—should be pronounced "ripper," but I'd much rather stick with "R-P-R," since calling it a "ripper" technique creates the wrong impression. Incidentally, the fact that dromaeosaurids are, ever since *Jurassic Park*, now regularly termed "raptors" makes discussion of this whole area more awkward than it should be. In ornithology, the term "raptor" is understood to be synonymous with "bird of prey."

See also *Deinonychus*; John Ostrom; *Jurassic Park*.

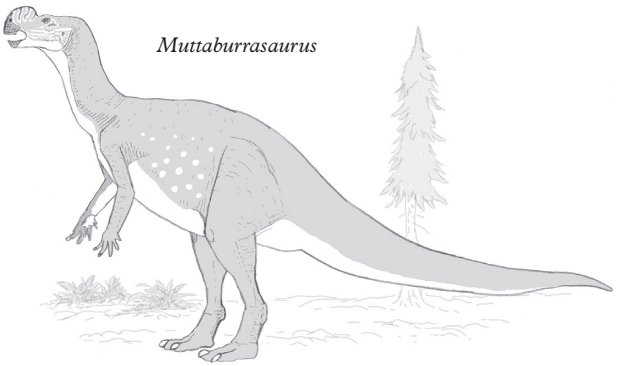
Rhabdodontomorphs

A Cretaceous iguanodontian ornithopod group—properly called Rhabdodontomorpha—that includes large and small species known from both Europe and Australia. The "core" members of this group are the rhabdodontids, all of which are robust, bipedal ornithopods unique to Europe. The rhabdodontid skull is broad across the cheeks, narrow at the beak, and includes

proportionally large cheek teeth that look suited for the slicing of tough plant material. The biggest rhabdodontids were 5–6 m (16–19.5 ft) long, but others were small (2–3 m [6.5–10 ft] long) and endemic to the islands that existed across Europe during the Late Cretaceous. A popular idea has been that these were "island dwarfs," their small size being a specialization for island life.

In some respects, rhabdodontids appear archaic relative to other Cretaceous ornithopods, so another popular idea has been that they were "living fossils" of their time, animals that had undergone little change across their history. This is a nice story, but it might be wrong. Several studies have found *Muttaburrasaurus* from the Early Cretaceous of Australia—named after the location in Queensland where it was first found—to be a close relative of the rhabdodontids. *Muttaburrasaurus* is large (about 8 m [26 ft] long), probably bipedal, and was equipped with a massive, hollow nose. The function of this big nose is unknown. Perhaps it was used in noise-making.

If *Muttaburrasaurus* and the rhabdodontids really do belong together, there's no firm indication that any of these dinosaurs really were "living fossils." In fact, their evolutionary history might have been dynamic. Maybe they started out large before some became small, maybe both *Muttaburrasaurus* and some rhabdodontids became large on independent occasion, or maybe something else happened altogether. Furthermore, this group almost certainly originated in or before the Middle Jurassic, around 170 million years ago. We can say this because the oldest members of related ornithopod groups are known from sediments of this age.



Yet, at the moment, the oldest rhabdodontomorphs are from the Early Cretaceous, and are about 130 million years old. The result is that we currently know nothing of the first 40 million years of rhabdodontomorph history, and we patiently await the discovery of Jurassic members of the group.

See also Ornithopods.

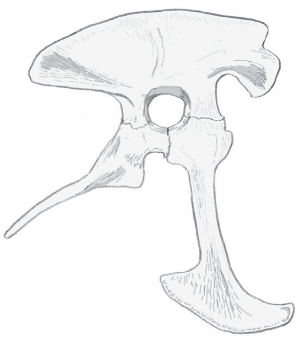
Saurischians

In "conventional" classifications, one of the two great dinosaur groups, the other being Ornithischia. Saurischians are, informally, the "lizard-hipped dinosaurs."

Saurischia was coined in a brief 1888 article by famously "defiant" and "anarchic" Victorian paleontologist Harry Seeley, who drew attention to the fact that those dinosaur species known at the time differed in several important respects, most obviously in hip structure. While ornithischians had pubic bones directed

down and backward, saurischians had pubic bones that projected down and forward. Seeley also noted that saurischians had air-filled (or pneumatic) bones and lacked armor. Two major groups form Saurischia: Theropoda and Sauropodomorpha.

Books on dinosaurs usually create the impression that Seeley's classification became the new, post-1888 standard, but in fact his proposal was ignored as long as he was alive. Not until 1907 did it win support from other specialists. The story on what happened over the following few decades is too complicated for this book, but by the 1970s, use of Seeley's Saurischia and Ornithischia was widespread. In a revolutionary 1974 article, Robert Bakker and Peter Galton made the argument that both groups shared a common ancestor, which was itself a dinosaur. A close link between theropods and sauropodomorphs did always seem logical, since the early members of both groups were lightly built, slender animals lacking the herbivorous specializations of ornithischians. The discovery of *Eoraptor* in 1993 emphasized this link, since here was a dinosaur that appeared to combine theropod and sauropodomorph features. Indeed, though published as a theropod, it wasn't long before some experts reidentified *Eoraptor* as a possible early sauropodomorph instead.



The problem with Saurischia, however, is that the hip shape regarded as

characteristic for the group is simply the "normal" configuration widespread across vertebrate animals. It isn't a special feature, found in theropods and sauropodomorphs alone. So, was Seeley's Saurischia really worthy of recognition? The idea that it might not be was raised a few times during the 1980s, in particular by those pointing to features suggestive of a link between ornithischians and sauropodomorphs (see the Phytodinosauria section). But in his 1986 study of dinosaur phylogeny, Jacques Gauthier succeeded in finding anatomical support for the reality of Saurischia: theropods and sauropodomorphs, Gauthier argued, shared features in the skull, neck, vertebral column, and hand not present in ornithischians. His case was strong and the reality of Saurischia has been supported ever since. . . .

Until 2017, the year in which Matthew Baron and colleagues published their proposal that theropods and ornithischians should be united within Ornithoscelida. According to this proposal, Seeley's Saurischia is not a clade. But rather than abandon the term Saurischia altogether, Baron and colleagues applied it to a herrerasaur + sauropodomorph clade. I think that this is a bad decision, since we're now stuck with more than one meaning of the word. As discussed elsewhere in this book (see the Ornithoscelida section), the exact status of Saurischia—as in, Seeley's version of Saurischia—is now uncertain. Some experts argue that its existence is no longer looking likely, others that its viability is dependent on which data we examine and how we examine it, and others that its existence was never in serious jeopardy.

See also Ornithischia; Phytodinosauria.

Sauropodomorphs

The long-lasting group—formally, Sauropodomorpha—that includes the giant, long-necked sauropods and their relatives. This is a diverse lot. It includes small, bipedal, short-necked predators in addition to large, long-necked, bipedal omnivores and quadrupedal herbivores, among which are the largest land-living animals of all time.

Sauropodomorphs started out during the Triassic as bipedal predators. An example is *Buriolestes* from the Late Triassic of Brazil, a meter-long (a little more than 3 ft) dinosaur, similar in appearance to early theropods, with recurved teeth and short arms. From ancestors like this, the sauropodomorph fossil record reveals a trend of increasing size, neck length, reliance on plant-eating, and robustness in the arms and hands.

Some Late Triassic sauropodomorphs (like *Melanorosaurus* from South Africa) reached 8 m (26 ft) in length and were mostly committed to life on all fours. They possessed proportionally long forelimbs, a straightened thigh bone (as opposed to a curved one), and a specialized lower arm where the hand was reoriented so that the palm faced backward, not inward as was typical for dinosaurs. The hands of animals like *Melanorosaurus* were shorter and more robust than those of earlier sauropodomorphs and were specialized for weight-bearing. Sauropods evolved from dinosaurs like this and continued not only an evolutionary trend of increasing size and neck length but also one in which the hands and feet became ever more specialized for weight-bearing.

Excepting sauropods, all the dinosaurs discussed here have conventionally been grouped together as

"prosauropods." You can still use this term if you want, but it's now ambiguous given that some "prosauropods" are today regarded as early sauropods. It can also be argued that the term "prosauropod" carries the implication that these animals were evolutionary prototypes, destined to evolve into sauropods. This just wasn't true: the majority of non-sauropod sauropodomorphs were neither ancestral to nor closely related to sauropods.

The key features used to unite sauropodomorphs have typically included an elongate neck, short skull, and tall teeth at the front of the mouth. These features were important in the group's history, but recent discoveries indicate that details of the jaw joint, upper arm, and hip joint might have been characteristic of the clade during the earliest part of its history. Most sauropodomorphs had pneumatic bones. This has conventionally been used to support the view that sauropodomorphs belong together with theropods in a clade termed Saurischia. However, a few other possibilities are now on the table, and if you want to know more about them, skip over to the Ornithoscelida and Phytodinosauria sections.

See also Prosauropods; Saurischians; Sauropods.

Sauropods

Most major dinosaur groups have a recognizable body shape, but none more so than the sauropods, the long-necked herbivorous giants of the Mesozoic. The earliest sauropods (examples include *Antetonitrus* from South Africa) lived around 200 million years ago, close to the Triassic-Jurassic boundary. The very last lived right at the end of the Cretaceous, 66 million years

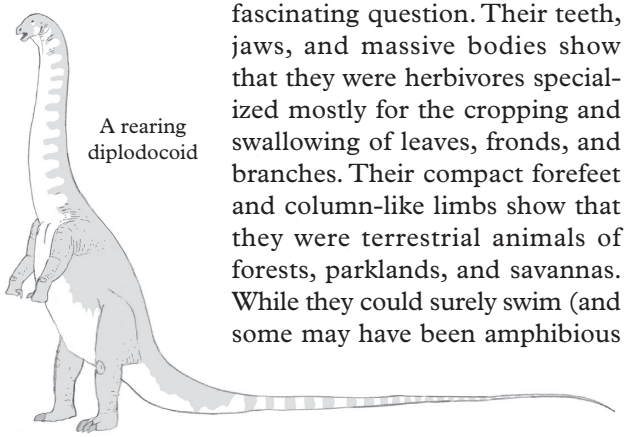
ago. Several different views have been put forward on sauropod origins and early history, but current thinking is that sauropods evolved from large quadrupedal sauropodomorphs like *Melanorosaurus* from the Late Triassic of South Africa.

Sauropods underwent an increase in size during the earliest stages of their evolution, and species 12–15 m (39–49 ft) long and around 7 tonnes (7.7 tons) in weight were already in existence by the Early Jurassic (that is, within the first 15 million years of the group's existence). Size is of course what sauropods are most famous for. A typical sauropod was around 12 m (39 ft) and 5 tonnes (5.5 tons), but species more than twice as big—25 m (82 ft) and more than 25 or even 50 tonnes (27.5 or even 55 tons)—evolved several times. The biggest include the Morrison Formation diplodocoid *Maraapunisaurus*, which was perhaps 35 m (115 ft) and probably over 70 tonnes (77 tons), and a selection of giant South American titanosaurs—*Argentinosaurus*, *Notocolossus*, *Patagotitan*, and others—all of which were 30–40 m (98–131 ft) and between 40 and 100 tonnes (44–110 tons). The precise size of the biggest sauropods remains controversial, in part because their remains are fragmentary, but also because different techniques for estimating weight give different results.

How and why sauropods got to be so big is a good question. Claims that their gigantism was a consequence of unusual global conditions (like lower gravity) are not supported by any evidence. The answer instead seems to be that sauropods combined a list of traits that predisposed them to gigantism. These include a highly pneumatized skeleton, a birdlike respiratory

system, an elongate neck that put a large quantity of food within easy reach, a reliance on hindgut fermentation (which becomes more efficient the bigger you are), and four columnar limbs suited for the support of massive weight. No other animal group has ever been equipped with this same combination of features, and this probably explains why no other land-living animal group reached comparable sizes. Even the very biggest ornithischians and extinct elephants and rhinos (like the famous *Paraceratherium*) failed to exceed 30 tons.

A vast amount could be written on our changing understanding of sauropod diversity and evolution. Several groups—including the archaic vulcanodontids, the especially long-necked mamenchisaurids, and the fairly average cetiosaurids—are outside Neosauropoda, the clade that includes the long-necked and long-tailed diplodocoids and the relatively short-tailed macronarians.



A rearing diplodocoid

How sauropods lived remains a fascinating question. Their teeth, jaws, and massive bodies show that they were herbivores specialized mostly for the cropping and swallowing of leaves, fronds, and branches. Their compact forefeet and column-like limbs show that they were terrestrial animals of forests, parklands, and savannas. While they could surely swim (and some may have been amphibious

animals of marshes, mangroves, or deltas), the idea that sauropods as a whole were aquatic swamp and lake dwellers—popular between the late 1800s and 1960s—was never based on good evidence or logic. This notion was partly contingent on claims that sauropods had weak jaws and teeth. In fact, their teeth were efficient cropping tools, specialized for the processing of relatively tough foliage. A large, mobile tongue and copious saliva probably helped during feeding.

The amazing sauropod neck—formed of between 12 and 19 vertebrae—was their key innovation, and experts agree that it gave sauropods access to a huge vertical and horizontal feeding envelope. Where experts disagree is how flexible the neck was and whether it was used to feed from low down or high up. Both the nature of the joints between the vertebrae and the way in which land-living animals habitually hold their necks show that sauropod necks were indeed flexible and that their necks were ordinarily held angled upward. While ornithischians and early sauropodomorphs could only feed on plants growing within 1–5 m (3–16 ft) of the ground, sauropods could feed from heights of 7–10 m (23–33 ft) with ease, and giant species must have had vertical reaches of 15 m (49 ft) and more.

There are also good reasons for thinking that some sauropods—diplodocoids in particular—could stand on their back legs while using the massive tail as a prop. Computer modeling and studies of bone strength show that bipedal rearing wasn't difficult for these dinosaurs, and they might have performed it whenever food was otherwise out of reach. But both neck flexibility and the kind of microscopic wear they have on their teeth show that some sauropods also foraged at ground level,

where they fed on ferns, herbs, and other low-growing plants. Short-necked sauropods such as dicraeosaurids were probably grazers rather than tree browsers.

Many questions about sauropod physiology and ecology remain. That incredibly long neck raises all sorts of questions about blood pressure, drinking, swallowing, breathing, and the nature of the nervous system. My personal take is that these animals—which lived worldwide for more than 130 million years—surely evolved *extreme* and remarkable solutions to life with this extreme and remarkable structure. We think that giraffes are remarkable because they possess a suite of unusual neck-themed specializations. I bet that sauropods were *even more remarkable*, and I mean no disrespect to giraffes by saying this.

When it comes to overall physiology, evidence for rapid growth in sauropods (especially when they were young) indicates that they were endothermic ("warm-blooded"). A few studies of isotopes preserved in sauropod teeth also indicate endothermy. An endothermic model for sauropod physiology is also consistent with the energetic value of the plants that were available to them, with the presence of organs and muscles that simply must have produced substantial quantities of heat, with a pneumatic system so extensive that it would have resulted in the internal movement of huge quantities of air (and thus the absorption of a large amount of oxygen), *and* with the existence of a neck that would been an excellent radiator of unwanted heat. Paleontologists have tended to dislike the notion of properly endothermic sauropods and have instead promoted a model called "inertial homeothermy," this being the idea that sauropods stayed warm simply by

virtue of being big. This doesn't explain fast-growing baby sauropods and persists mostly because the endothermic model has sometimes been implied to be implausible . . . which seems more of a preconception than something established by actual study.

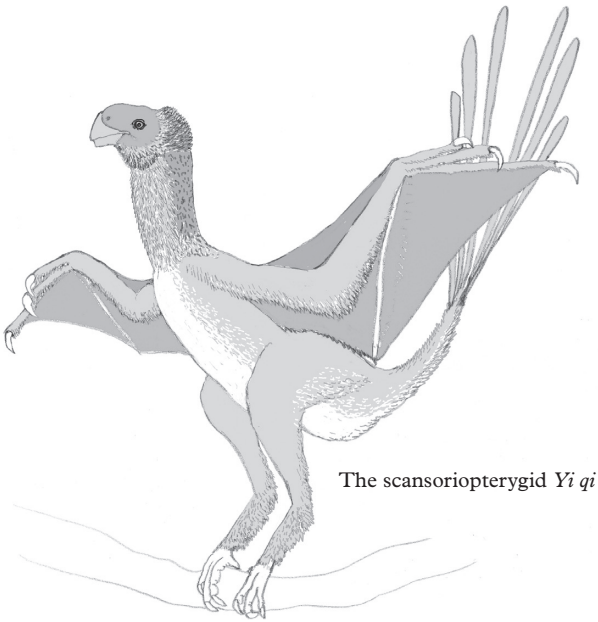
The final thing worth saying concerns sauropod ecology. There's little doubt that sauropods must have been what we call *ecosystem engineers*: movers and shakers of the Mesozoic terrestrial world, responsible for spreading seeds, fertilizing and overturning soil, cropping plants, and literally shaping habitats through their feeding and foraging activities. Their vast nesting colonies, the abundance of their hatchlings, and the energy provided by their bodies when they died were almost certainly key components of Mesozoic food webs. As remarkable as it might seem, most thoughts on these subjects are currently speculative: the fossil record simply isn't good enough to provide much insight on these ecological interactions, as crucial and far-reaching as they likely were.

It might be obvious from this summary that a whole book could be written about sauropod diversity, evolution, anatomy, behavior, and ecology. The good news is that such a book exists. I strongly recommend Mark Hallett and Mathew Wedel's 2016 *The Sauropod Dinosaurs: Life in the Age of Giants*.

See also Diplodocoids; Macronarians; Morrison Formation; Sauropodomorphs; Turiasaurs.

Scansoriopterygids

A maniraptoran clade of Middle and Late Jurassic China, noted for thrush- or pigeon-like size (as in,



The scansoriopterygid *Yi qi*

20–30 cm [8–12 in] or so), short-faced skulls, long fingers and . . . gliding membranes! Scansoriopterygids entered the scene in 2002 when *Epidendrosaurus* was published by Fucheng Zhang and colleagues. It's from the Tiaojishan Formation, a geological unit that seems to straddle the Middle and Late Jurassic in age. Zhang and colleagues regarded *Epidendrosaurus* as a long-tailed, tree-climbing, early member of Avialae, the bird clade. A second animal—*Scansoriopteryx*—was published at about the same time. It's now agreed that both are the same, and that *Epidendrosaurus* was published first.

The long third fingers of these little dinosaurs led to suggestions that they used them to extract insects from tree holes. This isn't a bad idea, but it's inconsistent with the fact that feathers grew from this finger. In fact, feathers were present across the body, as expected for maniraptorans. Another member of the group—*Epidexipteryx* (good luck with the pronunciation)—was published in 2008. Long, ribbon-like structures sprouted from the end of its short tail. These look like the display feathers of some modern birds, and it's likely that this is exactly what they are. If so, they show that this specimen was at (or close to) sexual maturity. And *Epidexipteryx* is, again, about thrush-sized, so it confirms that even adult scansoriopterygids were tiny.

Another surprise was revealed in 2015 when *Yi qi* was described. It had feathers and other features characteristic of the group but attached to its third finger was a *wing membrane*. A bony spike projecting from the wrist, termed the styliform element, helped support the membrane. Here was evidence that maniraptorans had experimented with membranous wings, an idea suggested here and there beforehand but never confirmed. *Yi qi* was big news, the result being a proliferation of artistic reconstructions. Just about all of them made this derpy, pigeon-sized creature into a black screaming nightmare dragon of death, whereas in reality it would surely have looked more like a grayish parrot. A second membrane-winged scansoriopterygid—*Ambopteryx*—was published in 2019.

How did these animals live? Their short skulls, downturned snouts and protruding teeth suggest insectivorous habits, but it might be that they were omnivorous

and maybe consumed fruits or seeds. Their fossils come from forested places, and the gliding membranes, small size and curved foot claws of *Yi* and *Ambopteryx* suggest that they, at least, were tree dwellers. Aerodynamic studies show that *Yi* and *Ambopteryx* were poor gliders, nor capable of flapping flight. There is, therefore, no good reason to think that they were occupying a "flying squirrel"-type lifestyle that involved the crossing of large gaps between trees, nor adapted for flying above the trees. Perhaps they were specialized for a lifestyle that involved short hops in cluttered, food-rich habitats.

As already mentioned, some studies have found scansoriopterygids to be early members of Avialae, and it's fair to say that this remains the consensus view. But arguably more interesting are suggestions that their affinities lie elsewhere, perhaps among oviraptorosaurs.

See also Maniraptorans; Oviraptorosaurs.

Sereno, Paul

Among the most famous paleontologists of the modern age, best known for his work on dinosaur origins, ceratopsians, spinosaurids, and Cretaceous birds. Sereno (born 1957) studied for his PhD under turtle expert Gene Gaffney and mammal expert Malcom McKenna at Columbia University in New York. To quote ceratopsian expert Peter Dodson, Sereno "created quite a stir as a graduate student" by hiking out to Mongolia to get access to the psittacosaurs and other ceratopsians he was interested in. He received his PhD in 1987. Sereno is one of a small number who brought cladistics (a new, rigorous way of analyzing evolutionary relationships) to dinosaur studies during the 1980s. Several of his early

papers—in particular his 1986 study of ornithischian evolution—were instrumental in establishing the nomenclature used for dinosaurs today.

During the early 1990s, Sereno published key papers on herrerasaurs and other Triassic dinosaurs, stegosaurs, Mesozoic birds, and early ornithischians, and later in the 90s he led studies on Cretaceous Saharan dinosaurs, including carcharodontosaurs, spinosaurids, and sauropods. The diversity of these studies make him well placed to produce reviews on dinosaur evolution as a whole, and he's probably produced more articles of this sort than any other modern specialist. Combine this with his interest in cladistics and nomenclature, and it's predictable that Sereno has proposed an enormous number of definitions for clades and the names associated with them. Indeed, the view of dinosaurs described throughout the book you're reading now owes a huge amount to Sereno's discoveries and publications.

Perhaps more so than any other paleontologist, Sereno's work has been accompanied by clever, well-orchestrated publicity. *National Geographic* and innumerable TV documentaries have featured his work. Not coincidentally, he was voted one of *People* magazine's 50 most beautiful people of 1997, surely an accolade every paleontologist aims for (that was a joke, they don't). This media-wrangling has caused some to dislike or criticize him, but the fact is that this showmanship has made him the well-funded and famous scientist he is today.

Sereno is currently professor of paleontology at the University of Chicago and a National Geographic Explorer in Residence. The work that's had him in the

press most recently is his 2014 paper (led by Nizar Ibrahim) on the anatomy and biology of *Spinosaurus*.

See also Carcharodontosaurs; Herrerasaurs; Macronarians; Marginocephalians; Ornithischians; Ornithopods; Spinosaurids.

Spinosaurids

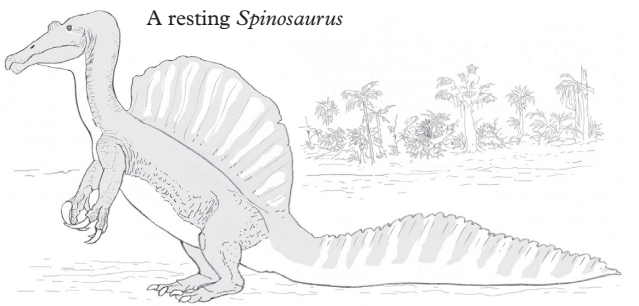
Among the most popular and controversial of dinosaurs, a group of long-skulled tetanurans generally agreed to be close to megalosaurids. Spinosaurids became known to science in 1915 when German paleontologist Ernst Freiherr Stromer von Reichenbach described the Late Cretaceous *Spinosaurus aegyptiacus* from Bahariya, Egypt. It was gigantic (perhaps 15 m [49 ft] long), and elongate bony spines show that it had a sail on its back. Little else was known, and Stromer assumed that *Spinosaurus* was shaped like *Megalosaurus* or *Allosaurus*. These fossils—mounted on the wall at the Bavarian State Collection of Paleontology in Munich—were destroyed during an Allied bombing raid of April 1944.

In 1984, French paleontologist Philippe Taquet noted that the lower jaw of Stromer's *Spinosaurus* was indicative of a long, crocodile-like skull. These comments were highly prescient. In 1986 the new spinosaurid *Baryonyx* from the Wealden of England was described, represented by remains more complete than those of *Spinosaurus*. *Baryonyx* didn't have a sail, but it did have a superficially crocodile-like skull, stomach contents showed that it ate fish, and its heavily muscled arms and massive, hooked hand claws look suited for the gaffing of large fish. The idea that spinosaurids were wading, fish-eating dinosaurs of wetlands now became

established. This was also our first look at a spinosaurid skeleton, and it proved that they looked quite different from how Stromer had imagined them.

Later discoveries made in northern Africa, Spain, Portugal, Brazil, Laos, and elsewhere have established that spinosaurids were widespread throughout the Early Cretaceous and early part of the Late Cretaceous. They seem to have disappeared around 95 million years ago. A possible Early Cretaceous spinosaurid vertebra is known from Australia, a Late Jurassic member of the group—*Ostafrikasaurus*, known from teeth alone—comes from Tendaguru, and a possible Middle Jurassic form (as yet unnamed) has been reported from Niger. These finds indicate that spinosaurids were present across Europe, Asia, and Gondwana, but it remains unclear whether they colonized Europe (and eastern Asia?) from Gondwana, or colonized Gondwana from a European center of origin.

Spinosaurids fall into two groups: the baryonychines of Europe and Africa (which lack sails and have a high lower jaw tooth count), and the spinosaurines of Africa,



A resting *Spinosaurus*

Asia, South America, and Europe (which have sails and possess retracted nostrils). The earliest stages of spinosaurid history remain shrouded in mystery, since we lack fossils that link them to other tetanuran clades. It's been implied that *Eustreptospondylus* from the Middle Jurassic of England might be close to spinosaurid ancestry, partly because it has a long face and a notch partway along the edge of the upper jaw. Other studies show that *Eustreptospondylus* is embedded within Megalosauridae, though, so this can't be right.

Spinosaurus itself has undergone quite the makeover since Stromer's time. In 2014, Nizar Ibrahim and colleagues argued that it had short hind limbs, webbed toes, a reduced hip girdle, and flexible tail, and that these features—combined with thickened, dense bone walls—made it an aquatic, swimming dinosaur, the proportions of which mean that it was perhaps quadrupedal when on land. It remains controversial whether this interpretation of *Spinosaurus* is accurate, since there are concerns that the bones used in this new reconstruction don't come from the same taxon. A vast amount has been written on this issue; it might be the most controversial topic in early twenty-first-century dinosaur science.

Whatever pans out, there *is* general agreement that spinosaurids were mostly exploiting aquatic prey. Their fossils come from places where large fishes were abundant, and isotopic data link them to aquatic resources. Much has been made of the fact that spinosaurids have crocodile-like faces; however, the crocodiles they most resemble are generalists that eat terrestrial prey as well as fishes, so it might be wrong to think that all spinosaurids were specialist fish-catchers all the time.

There's much more that could be said about these animals, enough for an entire book. At the time of writing, exciting new spinosaurid material from southern England is under study and should shed further light on the biology and anatomy of this interesting group.

See also Tetanurans; Wealden.

Stegosaurs

A mostly Jurassic and Early Cretaceous thyreophoran clade, famous for the paired spikes and plates arranged along the upper surfaces of the neck, back, and tail. The term stegosaur means "roofed lizard," a moniker initially chosen (by Othniel Marsh in 1877) because the plates were thought to form a turtle-like carapace. *Stegosaurus*—the most famous of the 24 or so recognized genera—is a large (7–9 m [23–29.5 ft] long) Late Jurassic stegosaur from the USA and Portugal, well known for its two rows of plates and for the two pairs of spines at the tail tip. Remarkably, the plates of *Stegosaurus* weren't symmetrical but arranged in an alternating or staggered arrangement. *Stegosaurus* seems to be an unusual stegosaur. The majority were smaller (more like 4–6 m [10–19.5 ft] long) and equipped with more spikes, or at least pointed, conical plates rather than big, flattened plates.

Stegosaur hind limbs are longer than their forelimbs and their hips are wide, indicating enormous guts and a hindgut fermentation style of dealing with food. The stegosaurian skull is generally broad and deep in its posterior half, but narrow (and sometimes shallow) at the front. Stegosaur teeth are tiny, their crowns shaped like leaves with serrated margins, but computer

modeling shows that their bite force was similar to that of browsing and grazing mammals. These features indicate that stegosaurs were selective feeders which browsed on leaves, fronds, and branches within about a meter of the ground. The possibility that they could rear up bipedally (perhaps using the tail as a prop) has been proposed and, if valid, would mean that they could also feed at heights of 3–4 m (10–13 ft).

Older illustrations and museum-mounted skeletons of stegosaurs show an arched back, a down-sloping neck and tail, and a head just centimeters off the ground. Articulated skeletons and the poses adopted by living

animals show that these reconstructions are inaccurate, and that the tail should be near-horizontal and well up off the ground, while the neck should curve upward. The head was probably ordinarily held level with the back, if not higher. The stegosaur neck is not short and was long in a few kinds, most famously *Miragaia* from Portugal.

The function of stegosaurian plates and spikes (those of *Stegosaurus* in particular) has been the source of debate, as is always the case for extravagant structures in dinosaurs. A defensive role for the plates is unlikely, as they weren't well placed for this role. Suggestions that they might have helped with temperature control are interesting and can't be dismissed given that all kinds of structures that project from animals' bodies (head crests, ears, antlers, dewlaps, and so on) function in heat loss. However, the fact that stegosaur taxa differed markedly in the size, shape, and number of their plates *and* that the plates grew at an unusually rapid rate relative to the rest of the skeleton indicates that the plates evolved as ornaments: as structures used to signal maturity and condition. They could have been boldly patterned and brightly colored, and we might imagine stegosaurs deliberately parading their bodies, broadside, during the breeding season.

The spikes at the tail tip were certainly weapons, maybe used in battles with mating rivals as well as against predators. A few theropod bones possess holes that look like they were caused by stegosaur tail spikes, and computer modeling shows that the tail was flexible enough to throw the spiked tip far to the side and also up and down quite a way. In a 1982 cartoon,

Gary Larson made the whimsical suggestion that the spiked tail tip might be termed a thagomizer. Some anachronistic cavemen are learning about stegosaurs and we see that the tail tip is so named "after the late Thag Simmons." Some dinosaur experts argue that this name is sufficiently useful and memorable that we should adopt it as part of technical lexicon. Others—like stegosaur expert Susie Maidment—think that it's silly and jokey and that we shouldn't use it. I'll go with majority opinion, whatever that is.

See also Thyreophorans.

Sue

Only a few fossil dinosaurs can be considered familiar as individuals. Dippy the *Diplodocus* of London's Natural History Museum is one, and Sue the *Tyrannosaurus rex* is another. Sue resides at Chicago's Field Museum and has a famously tumultuous history. Despite the name, Sue—who has an active social media life on Twitter—does not identify as female and is instead gender neutral. The name was, however, awarded at a time when the specimen was thought to be female, on which read on.

Sue's story starts in August 1990 when an exceptionally complete, big *T. rex* was discovered in the Black Hills of South Dakota by commercial fossil collector Sue Hendrickson. Hendrickson alerted Pete Larson, president of the Black Hills Institute, who arranged the fossil's excavation. A dispute over ownership then erupted since the landowner—a member of the Sioux named Maurice Williams—argued that the fossil belonged to him, leading to the most cleverly named

article of the entire saga ("Will the Sioux Sue for Sue?"). The specimen then became within the jurisdiction of the FBI, which raided the Black Hills Institute, confiscated Sue, and transferred it to the South Dakota School of Mines and Technology. A lengthy court case ensued, the end result of which is that Sue went up for auction on October 4, 1997.

Concerned that Sue might disappear into private ownership, the Field Museum formed a consortium with private individuals, Disney, McDonald's, and the California State University System and ended up winning. The final fee—agreed within ten minutes of the auction's start—was US$8.3 million. Sue had been secured for the public trust.

Years of preparation work then occurred in specially built laboratories at both the Field and Disney's Animal Kingdom in Orlando. And by 2000, the specimen—officially FMNH PR2081 (learn to say this, it's cooler than "Sue")—was mounted for display in the Field's main entrance hall. A full anatomical description of the specimen, written by paleontologist Chris Brochu, appeared in 2003. It showed that several claims made about the specimen (that it was female, that it preserved bite marks and even embedded tooth fragments from other *T. rex* individuals, *and* that it was preserved adjacent to the remains of one or two of its juveniles) couldn't be substantiated. Brochu's study also succeeded in finally putting the detailed anatomy of *T. rex* on record. Believe it or not, this hadn't been done before.

More recently, Sue was removed from display in the Field's main hall and given its own dedicated exhibit,

which opened in 2018. This move was performed in conjunction with a remounting of Sue's skeleton, the most notable change involving the addition of the specimen's complete set of belly ribs, technically termed gastralia. These demonstrate the massive depth of the body cavity, something which was always there but not previously easy to appreciate.

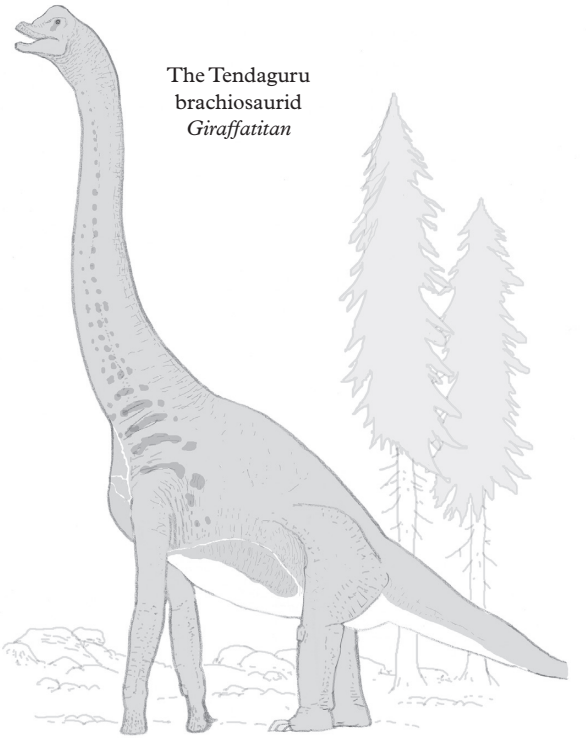
See also *Tyrannosaurus rex*.

Tendaguru

One of the world's Top Ten dinosaur-bearing Mesozoic sites (and by far the best on the entire African continent), Tendaguru in Tanzania has yielded abundant Late Jurassic dinosaurs. These include the theropod *Elaphrosaurus*, the brachiosaurid *Giraffatitan*, the diplodocoid *Dicraeosaurus*, the stegosaur *Kentrosaurus*, and the ornithopod *Dysalotosaurus*. Fragmentary remains indicate the presence of spinosaurids, carcharodontosaurs, turiasaurs, and mamenchisaurids too.

This assemblage has rough similarities with that of the USA's Morrison Formation, and a popular idea for much of the twentieth century was that both regions (and presumably those in between) shared the same dinosaurs. Recent work demonstrates a more complex pattern and shows that Tendaguru and Morrison dinosaurs aren't so similar after all. The regions might share major clades (like Brachiosauridae, Stegosauridae, and Dryosauridae), but not genera. In fact, the two had been separated for nearly 20 million years by the time the Tendaguru dinosaurs were alive, so they were actually highly distinct.

The dinosaur-bearing stratigraphic unit at Tendaguru —the Tendaguru Formation—is thick and represents an impressive 35 million years of sediment laid down between the Middle Jurassic and Early Cretaceous. However, the dinosaurs of the formation come from the Kimmeridgian and Tithonian parts of the Late Jurassic, making them between 157 and 145 million years old.



The Tendaguru brachiosaurid *Giraffatitan*

The backstory to the Tendaguru dinosaurs has been told often enough, but usually in a way that misses key information. During the early 1900s, Tanzania was the German colony Deutsch Ostafrika, and the conventional story has it that German engineer Bernhard Wilhelm Sattler was—in 1906—the first to discover dinosaur bones here. Expeditions carried out between 1909 and 1913 resulted in a vast haul of specimens, all of which were shipped to Berlin where—assembled between the two world wars, during a time of extreme economic hardship—they formed the centerpiece to the spectacular Museum für Naturkunde. After WWI, Germany "lost" ownership of Tanzania (now known as Tanganyika) to Britain, and it wasn't long before British teams also excavated at Tendaguru. They recovered more dinosaurs, but only in recent years have studies of these specimens appeared in print.

Today, it's difficult to look at all this colonial European activity as anything other than the plundering of Tanzania's paleontological wealth and heritage, and calls for the fossils to be repatriated have increased in volume and frequency in recent years. Discussions are ongoing at the time of writing. It's also clear that the story positing Tendaguru's discovery as being entirely thanks to German luck and fortune is not true and perhaps even a deliberate attempt to exclude local people from the narrative. Far from being unaware of the fossils, they used them in religious ceremonies and actually led European visitors to the relevant locations.

An excellent guide to the history of fossil collecting at Tendaguru—the book *African Dinosaurs Unearthed*—was published by Gerhard Maier in 2003. It's an impressive,

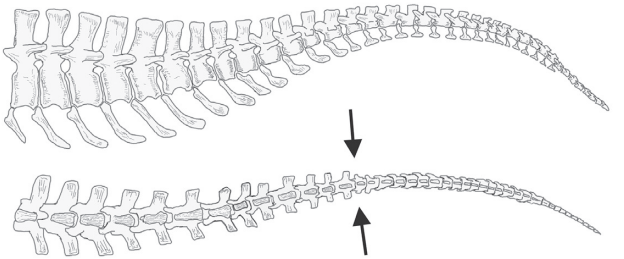
weighty work that covers the story in considerable detail, but sources tell me that the original manuscript was fully twice as long as the final product.

See also Brachiosaurids; Morrison Formation.

Tetanurans

A major theropod clade—properly Tetanurae—originally named to be the sister-group to Ceratosauria, and intended to contain megalosauroids, allosauroids, and coelurosaurs . . . though read on. The name Tetanurae was published by Jacques Gauthier in a 1986 study which did much to establish our modern understanding of dinosaur evolution. It means "stiff tails" and refers to the presence of overlapping processes on the tail vertebrae that stiffen the tail's end third. A name intended to include the same set of animals—Dinoaves—was published by Bakker in 1986 but never caught on.

A list of anatomical features is typical of tetanurans: the teeth are all in front of the eye socket, the air-filled openings on the side of the snout are more extensive than those of more archaic theropods, the bones of the



A tetanuran tail skeleton, from the side and (below) from above, to show the location of the transition point

fourth finger are reduced, the hand is proportionally long, and the shoulder blade is slender. As usual, many of these features were modified in certain lineages later in their history. On that note, we tend to imagine a typical tetanuran to be a big, predatory animal, 7 m (23 ft) long or so, like *Megalosaurus* or *Allosaurus*. But the group also includes the coelurosaurs, a group whose diversity in size, shape, and lifestyle exceeds that of all other theropods put together.

In the tetanuran tail, the sideways-projecting bony flanges called transverse processes continue for less of the tail's length than they do in other dinosaurs. The point at which the transverse processes disappear—termed the transition point—gradually crept closer to the body during tetanuran evolution. The transition point's position is related to the extent of the muscle called the caudofemoralis longus, or cfl for short. This is the huge muscle, attached both to the bony flange called the fourth trochanter on the femur *and* to the lower surface of the tail skeleton, that pulls the leg backward during locomotion. The reduction of the cfl is especially obvious in coelurosaurs. Over time, the entire tail became reduced, a trend carried to its extreme in birds.

As originally used, the term Tetanurae was intended to be synonymous with the "megalosauroid, allosauroid, coelurosaur" clade. Ceratosaurs were very much not part of the group. But in recent years there's been a tendency to expand its use such that ceratosaurs like abelisaurids are regarded as tetanurans too. I don't think that this is ideal, but oh well.

See also Allosauroids; Ceratosaurs; Coelurosaurs; Megalosauroids.

Therizinosaurs

Properly Therizinosauroidea or Therizinosauria, a mostly Cretaceous coelurosaur clade so unusual that they've been described as dinosaurs designed by committee. Today we know that therizinosaurs are maniraptorans, and likely one of the oldest lineages within the group. We also know—thanks to *Beipiaosaurus* from Liaoning—that they were feathered (as expected for maniraptorans), perhaps with a shaggy plumage mostly formed of hairlike filaments. Spinelike structures were also scattered throughout the plumage. The small, leaf-shaped teeth and beaked tips to the jaws look suited for a diet of leaves, though it might be that fungi, insects, and fruit were eaten too.

Therizinosaur proportions are unusual. They tended to have a long, robust neck, broad pelvis, stocky hind limbs, broad feet, and short tail. These features indicate that they maintained a more erect posture than typical for dinosaurs. They were likely high-browsing herbivores which used their large hand claws in manipulating foliage, as well as in self-defense and perhaps display.

This is our modern take on these animals. But it's taken decades to get to this point, and the story describing how we got here is interesting. Things began in the 1950s when Russian paleontologist Evgeny Maleev described a Late Cretaceous reptile known from ribs, bones from the foot, and some massively long hand claws, the longest of which were 70 cm (2 ft) long. He named it *Therizinosaurus cheloniformis*, meaning "turtle-like scythe lizard," and thought it was an aquatic, turtle-like animal. By 1970, Anatole Rozhdestvensky—another Russian paleontologist—had realized that

Therizinosaurus was a theropod, perhaps an ant-eating form that used those giant claws to break open insect nests. This ant-eating idea continued to raise its proverbial head over the years but isn't consistent with the bulk of data (specialized ant-eaters are way smaller than therizinosaurs and have a suite of cranial features not seen in this group).

We then move to 1980, when Rinchen Barsbold and Altangerel Perle described a group of Late Cretaceous Mongolian dinosaurs which they called segnosaurs. The group included *Erlikosaurus*—named for a complete skull—and *Segnosaurus*, based on a lower

Therizinosaurus

jaw, limb bones, a pelvis, and some vertebrae. Barsbold and Perle thought that the beaks, small teeth, and broad feet of segnosaurs showed that they were amphibious predators of fish. By 1982, Perle argued that *Therizinosaurus* was a segnosaur, a consequence being that Therizinosauroidea—rather than Segnosauria—is the oldest name for the clade.

The broad feet of therizinosaurs are unusual relative to those of other theropods and it was this fact above all others which, in 1984, led Greg Paul to contest the theropod hypothesis otherwise favored at this point. Paul argued that therizinosaurs had much in common with sauropodomorphs like *Plateosaurus*, yet were ornithischian-like in jaw and ankle anatomy. He therefore proposed that therizinosaurs were late-surviving relicts of the sauropodomorph-ornithischian transition. . . . which makes sense only if you accept the Phytodinosauria model of dinosaur affinities. This idea didn't win adherents and ran counter to the consensus emerging on dinosaur phylogeny at the time, but Paul's take on therizinosaur anatomy—it basically had them as modified plateosaurs, with beaked jaws and massive hand claws—appeared in several books of the time and was the "go to" view on these animals for a few years.

Later in the 1980s, a few authors proposed sauropodomorph affinities for therizinosaurs. It was the theropod idea, however, that won out. In their 1993 description of the Chinese therizinosaur *Alxasaurus*, Dale Russell and Zhi-Ming Dong supported a position for these dinosaurs deep within Theropoda, and—in a surprise move—close to maniraptorans. A maniraptoran position for therizinosaurs was supported by later

studies and bolstered by new discoveries, among them *Beipiaosaurus* (published in 1999) and *Falcarius* from the Early Cretaceous of Utah (published in 2005). *Falcarius* is interesting because it's proportioned more like a standard coelurosaur than other therizinosaurs.

Russell might well have "got therizinosaurs right" when it comes to phylogeny, but another interesting diversion in thoughts on these dinosaurs came from his 1993 attempt to reconstruct therizinosaur appearance and behavior. Working with Donald Russell and artist Ely Kish, Russell argued that therizinosaurs were convergent with chalicotheres, a group of clawed, long-armed herbivorous mammals. By combining the skeletal parts known from various therizinosaurs and making extrapolations to account for size, the team proposed that *Therizinosaurus* was probably toothless, had a broad, short body, short hind limbs, a disproportionally long neck, and that the hand claws reached the ground and were used as props. They described how *Therizinosaurus* was likely adapted for sitting while reaching into foliage with the neck. An interesting interpretation of therizinosaur appearance and biology, to be sure, but one best considered only roughly correct.

Little direct evidence exists on therizinosaur biology. Embryos and eggs are known, as are footprints. Alas, none of these things tell us much beyond what we'd guess already. A 2013 study of bite strength in *Erlikosaurus* concluded that the bite was weak and that its jaw actions involved mostly cropping and leaf-stripping.

If therizinosaurs are one of the oldest clades within Maniraptora, it follows that they must have been in existence from the Middle Jurassic at least (since we

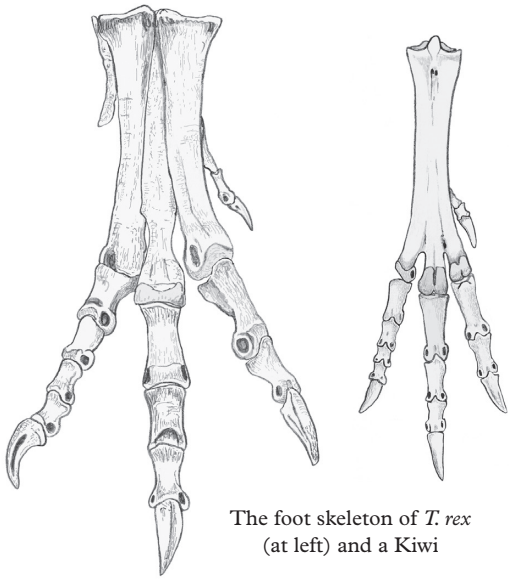
know of early members of the bird clade that date to that time). At the time of writing, Jurassic therizinosaurs are all but unknown. What might be an Early Jurassic therizinosaur is known: *Eshanosaurus* from southwest China, known only from a partial lower jaw. The identity of this specimen is controversial. Some argue that it's a sauropodomorph, but another possibility is that it's not from the Early Jurassic at all but from Cretaceous sediments. If it *is* an Early Jurassic therizinosaur, it shows that several major events in maniraptoran and coelurosaur evolution occurred during the first half of the Jurassic, which is earlier than otherwise thought.

See also Coelurosaurs; Maniraptorans; Phytodinosauria.

Theropods

Predatory dinosaurs—not all of which were predatory (read on)—and birds are united within Theropoda, the key feature of which is a narrow, birdlike foot. Theropods have more air-filled cavities in the skull than do other dinosaur groups, a wishbone or furcula, and a hand in which the fifth finger is reduced or absent. As usual, these features aren't present in all taxa across the group but became modified or lost in various lineages. Theropods survive to the present and are thus the longest-lived dinosaur clade. And indeed, the diversity, biomass, and distribution of birds mean that theropods can be described as the "most successful" dinosaur clade of all.

Those theropods usually regarded as most typical—animals like *Megalosaurus* and *Allosaurus* from the



The foot skeleton of *T. rex* (at left) and a Kiwi

Jurassic—were big bipedal predators with a deep, narrow skull, recurved, serrated teeth, and muscular forelimbs equipped with large, recurved claws on the inner three fingers, the largest of which was on the thumb. The theropod neck is usually flexible and powerfully muscled, the legs are built for sustained walking or running, and the hip girdle is deep and narrow, with down-and-forward-pointing pubic bones that sometimes have a large boot-shaped extension at their conjoined ends. All these features were modified during theropod history, though. Some evolved especially long arms (a trend culminating in avian wings), or short legs, or widened hips where the pubic bones ended up

pointing down and backward (which is what they do in birds). Toothlessness evolved on several occasions.

Several small, primitive dinosaurs of the Triassic are the oldest of theropods. These dinosaurs—*Eodromaeus* from Argentina is an example—were about 1 m (3 ft) long with grasping hands, lightweight proportions, and a rectangular skull. Animals of this sort gave rise to the clade that contains all remaining theropods, among which are ceratosaurs and tetanurans, the latter being the so-called stiff-tailed theropods, the highly diverse clade that contains the majority of theropod taxa. Tetanurans include an assemblage of mostly midsized and large predatory theropod clades—the megalosauroids and allosauroids—as well as the coelurosaurs, the clade that includes birds and all remaining birdlike tetanurans. All of these groups get their own sections in this book.

"Typical" theropods like *Megalosaurus* and *Allosaurus* were predators that used their teeth and powerful jaws to take bites from prey. They perhaps made slashing wounds or tears on the bodies of prey animals to weaken them before starting to feed. The strongly muscled arms and recurved hand claws might have been used to create wounds too. Numerous other feeding styles evolved throughout theropod history. The crocodile-like heads of spinosaurids were likely used in grabbing fish as well as terrestrial prey, tyrannosauroids evolved a crushing bite that could be used to break open bones, and the toothless jaws and slender, lightweight necks of some coelurosaurs allowed them to browse from vegetation or pick up small prey items. Some coelurosaurs—most famously *Velociraptor* and its

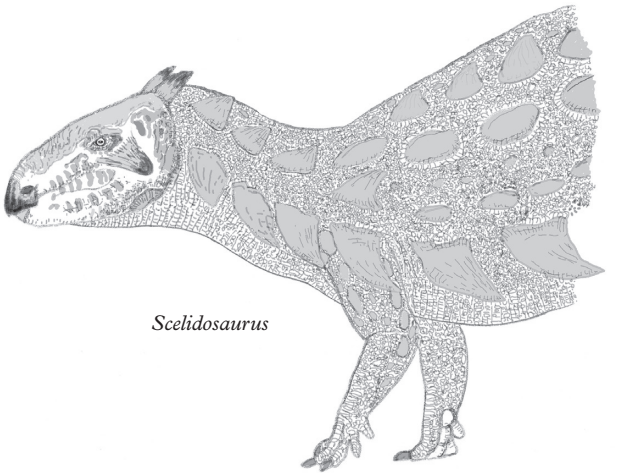
kin—transitioned to use of their flexible, sharp-clawed feet as their primary weapons. Birds have evolved a phenomenal diversity of foraging and feeding styles that include filter feeding with a modified bill, fruit eating, mud probing, insectivory, and *Velociraptor*-like use of taloned feet.

See also Allosauroids; Ceratosaurs; Coelurosaurs; Megalosauroids; Tetanurans.

Thyreophorans

The armored and plated ornithischians—ankylosaurs and stegosaurs and their closest relatives—are united within Thyreophora, a name that means "armor bearers." The majority of thyreophorans were quadrupedal and—with one or two exceptions—herbivorous. The exceptions to the quadrupedal rule are the oldest members of the group. Among these is *Scutellosaurus* from the Early Jurassic of the USA, a small, lightly built, lightly armored, long-tailed dinosaur. A second possible example is the small, bipedal, unarmored *Lesothosaurus* from the Early Jurassic of southern Africa. *Lesothosaurus* was found in a 2008 study to be a thyreophoran close to the ancestry of the whole clade. If this is correct, it's no longer the case that all thyreophorans are armored.

Excepting *Lesothosaurus*, thyreophorans share parallel rows of horn-covered bones, termed osteoderms, located along the upper surface and sides of the neck, body, and tail. These were altered a great deal during evolution, such that massive shoulder spines, giant, upward-projecting bony plates, and other structures evolved in some thyreophoran clades. It's obvious that



Scelidosaurus

these diverse, modified osteoderms didn't all have the same function. Some—like the closely spaced, rectangular osteoderms of many ankylosaurs—probably functioned as protection against theropods, but others could have been used in mating displays or battles, in collecting or shedding heat, in camouflage, or even in digging or foraging. Rhinos, deer, and elephants use horns, antlers, and tusks to break branches and tear off bark; it could be that thyreophoran spikes and spines were sometimes used similarly.

Thyreophorans of many kinds have been known to science since the late 1800s. In fact, Early Jurassic *Scelidosaurus* from England—the first non-bird dinosaur known from a good, articulated skeleton–was named by Richard Owen in 1859, back when the concept of dinosaurs was still new. *Scelidosaurus* can basically be

imagined as a more heavily built, more extensively armored, enlarged version of *Scutellosaurus* (it was about 4 m [13 ft] long, compared with the 1.2 m [4 ft] of *Scutellosaurus*), and it was probably close to the ancestry of both stegosaurs and ankylosaurs. These two groups were frequently classified together during the 1800s and early 1900s, a popular idea for a while being that ankylosaurs were late-surviving stegosaurs. Today we think that stegosaurs and ankylosaurs shared an ancestor, one that must have been alive during the Early Jurassic, around 175 million years ago.

When it comes to the evolutionary position of thyreophorans as a whole, the view popular for much of the twentieth century was that they'd emerged early in dinosaur history from ornithischians regarded at the time as ornithopods. In 1915, Hungarian paleontologist and nobleman Baron Franz Nopcsa proposed that ankylosaurs, stegosaurs, and ceratopsians should be classified together in a group termed Thyreophora. His proposal was essentially ignored until the 1980s. Several studies—most published between 1984 and 86—"discovered" Thyreophora anew, albeit in a form which excludes ceratopsians. More recent work has confirmed this view and established that thyreophorans represent a great arm of the ornithischian family tree very much distinct from the one that includes marginocephalians and ornithopods.

See also Ankylosaurs; Ornithischians; Stegosaurs.

Titanosaurs

The most speciose, successful, and widespread of sauropod clades. Titanosaurs are named for *Titanosaurus*,

named in 1877 for a tail vertebra from the Late Cretaceous of India. This vertebra is interesting because it's procoelous, which means that it's concave at the front and convex at the rear, the result being the presence of ball-and-socket joints between the vertebrae. Thanks to this configuration, it's been suggested that titanosaurs had flexible, even prehensile tails. Such ideas aren't favored today because they ignore the muscles and other tissues that would have surrounded the bones. Vertebrae of this sort—known from England, France, Argentina, and elsewhere—have turned out to be present in several titanosaur taxa. Accordingly, *Titanosaurus*—the original titanosaur—is not currently recognized as a valid taxon.

The good news is that other members of the clade (some with procoelous tail vertebrae, some not) are comparatively well known. These include the long-necked *Rapetosaurus* from Madagascar, *Saltasaurus* from Argentina, and the stocky *Opisthocoelicaudia* from Mongolia. Ah yeah, *that* name. *Opisthocoelicaudia* is named for its tail vertebrae. These are opisthocoelous, meaning concave at the back, and convex at the front, the opposite of that present in the original *Titanosaurus* specimen! All the titanosaurs mentioned so far are from the Late Cretaceous, but we know of probable Early Cretaceous taxa from Brazil, Malawi, Russia and Europe.

Because the majority of titanosaurs are from the Gondwanan continents, it's usually been thought that the clade originated in the south and only moved north (into North America, Europe, and Asia, apparently independently) at the end of the Cretaceous. However, a growing record of Eurasian titanosaurs from the first

half of the Cretaceous is challenging that view, and at the time of writing it's not quite clear what the story is.

The shape of the titanosaur family tree is confusing. A series of archaic taxa with relatively simple vertebrae, the andesauroids and kin, are outside a clade called Lithostrotia. This contains those titanosaurs with horn-covered bony lumps in their skin, properly called osteoderms (the name Lithostrotia means "inlaid with stones"): more on those in a moment. Numerous subdivisions have been named within Lithostrotia. Among those mentioned most often are Lognkosauria, the members of which are noted for their massively broad, thickened vertebrae, and Saltasauridae, a clade that contains small and midsized South American taxa and, probably, the North American *Alamosaurus* and Asian *Opisthocoelicaudia*.

Titanosaurs varied tremendously in size, the smallest being similar to modern cattle or horses, and the biggest being among the biggest sauropods of all. *Argentinosaurus*, *Patagotitan*, *Notocolossus*, and other super-giants (all of which probably belong within Lognkosauria) were around 30 m (98 ft) long and weighed somewhere between 40 and 100 tonnes (44–110 tons). Most titanosaurs were broad across the hips and body, with more widely spaced hands and feet than other sauropods. This is confirmed by trackways that show so-called wide gauge gaits. The shapes of the limb bones, and their muscle attachment sites, indicate that titanosaurs were comparatively agile, able to traverse hilly terrain, and rear bipedally.

Titanosaurs varied a lot in skull shape, limb proportions, and neck and tail length. Good skull material

The giant titanosaur *Patagotitan*

is rare, but well-preserved specimens reveal a broad, rounded snout that's much shallower than the section housing the eyes and brain. The teeth are slender and pencil-shaped in some taxa but broader-crowned in others. As mentioned above, titanosaurs within Lithostrotia possessed oval or rounded osteoderms across the back and sides. The function of these structures isn't certain. They might have served a defensive role, but

an alternative is that they were used as a calcium store, utilized by these dinosaurs (specifically by females) in the production of eggshell.

See also Macronarians.

Turiasaurs

A recently recognized sauropod clade—formally Turiasauria—originally thought restricted to the Jurassic of Europe. Turiasauria is named for *Turiasaurus* from the Late Jurassic of Spain, which, when published in 2006, won a lot of news coverage: with a possible length of 30 m (98 ft), it's one of the largest of all sauropods. Yet it's from Spain, not Argentina as is generally expected for mega-sauropods. *Turiasaurus* has massive nostrils, a large bony crest at the top of its humerus, and vertebrae that lack some of the bony struts and other structures present in some other sauropod groups. These features suggest that turiasaurs are not part of Neosauropoda, the great clade that includes diplodocoids and macronarians. Those massive nostrils, however, do give turiasaurs a macronarian-like look, and it's possible that they might turn out to be part of that clade.

Turiasaur teeth are spatulate and those from the back of the jaws have unusual crowns. These are vaguely shaped like an inverted heart, with the pointed part of the "heart" being the crown's apex.

Two other Spanish sauropods—*Losillasaurus* and *Galveosaurus*—also seem to be turiasaurs, and a fourth taxon (*Zby* from Portugal) was named in 2014. Could turiasaurs be endemic to the Iberian Peninsula? That would be consistent with the archipelago-like nature of the region at the time. But . . . no. Today we know

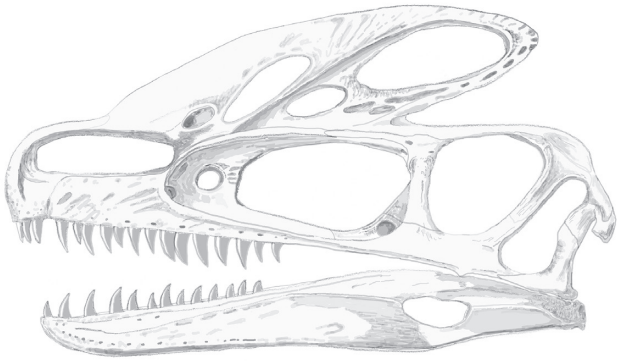
of turiasaurs from the Middle Jurassic of England, the Late Jurassic of Switzerland, the Early Cretaceous of the USA, and the Wealden. It also seems that *Tendaguria* from . . . Tendaguru, of course—previously regarded as a titanosaur or near-titanosaur—is a turiasaur too. The fact that turiasaurs are known from the Middle Jurassic shows that they were present at a time prior to the fragmentation of the supercontinent Pangaea, so it might turn out that they were globally distributed.

See also Diplodocoids; Macronarians.

Tyrannosauroids

The coelurosaurian clade—properly Tyrannosauroidea, sometimes called tyrant dinosaurs—that includes *T. rex* and its large, short-armed kin (the tyrannosaurids) in addition to various smaller, longer-armed species. The most familiar tyrants are animals of the Late Cretaceous, but the oldest are from the Middle Jurassic. These older tyrants include *Proceratosaurus* from England and *Kileskus* from Russia, both of which are part of the archaic clade Proceratosauridae, most or all of which had horns or nasal crests.

Key tyrant features include incisor-like teeth at the front of the upper jaw, a reinforced, thickened midline to the top of the snout, and long, slender hind limbs. Several trends are apparent in tyrant evolution: body size increased, the skull became larger and more powerful, and the forelimbs reduced in size and changed from the ancestral three-fingered configuration to a two-fingered one. These changes indicate increased reliance on the jaws and teeth and on biting overall,



Crested skull of the proceratosaurid *Guanlong*

and decreased reliance on use of the arms. It would be misleading, however, to regard these trends as true for all tyrant clades. Several midsized tyrants—like *Dryptosaurus* from the Late Cretaceous of New Jersey (it was about 7.5 m [24.5 ft] long)—retained powerful, formidably clawed forelimbs. Long filaments preserved on *Dilong* and *Yutyrannus* (both of Liaoning Province in China) show that some tyrants were fuzzy or feathery, and it remains contentious whether this was true for giants like *T. rex*.

The tyrants of the Jurassic and Early Cretaceous were generally less than 3 m (10 ft) long and were mostly "mid-tier" predators living in habitats dominated by megalosauroids and allosauroids. An extinction event that happened around 95 million years ago in the middle of the Cretaceous mostly removed those groups, and it seems that this allowed tyrants to evolve larger body size and occupy the top predator roles.

They didn't fight their way to the top by being inherently awesome, sorry.

Prior to the 1990s it was generally thought that tyrants were closely related to allosauroids, and that shared features like a proportionally large skull united these predators within a group termed Carnosauria. But tyrants are actually more like ostrich dinosaurs and other lightly built theropods in the pneumatic details of their vertebrae and the slender proportions of their feet, so a different view—placing them within Coelurosauria—emerged around 1996. This had been proposed way back in the 1920s by Friedrich von Huene in Germany, and independently by William D. Matthew and Barnum Brown in the US, but fell out of fashion during the middle of the twentieth century. It has since been confirmed in numerous studies, the majority of which find tyrants to be one of the oldest coelurosaur clades.

A flurry of discoveries made since 2001 have added great complexity to the tyrant family tree. Proceratosaurids are outside the clade that includes several relatively small Jurassic and Early Cretaceous taxa—*Juratyrant*, *Dilong*, *Eotyrannus*, and so on—in addition to the big-bodied eutyrannosaurs. Eutyrannosaurs include several midsized, North American tyrants in addition to Tyrannosauridae proper. Tyrannosauridae proper contains the North American albertosaurines, the long-snouted, Asian *Alioramus*, and the robust North American *Daspletosaurus* and *Tyrannosaurus* and Asian *Tarbosaurus*. An enigmatic theropod clade of the Gondwanan continents—the megaraptorans—might also be members of Tyrannosauroidea. There's

so much to say about megaraptorans that they get their own section in the book.

See also Coelurosaurs; Megaraptorans.

Tyrannosaurus rex

Few animal species are familiar enough to be known by their two-part scientific name. The Boa constrictor (properly, the Common boa) is one. *T. rex* is the other.

In part, *T. rex* owes its fame to happenstance. It was discovered early in paleontological history, was written about by scientists who adored the vigorous promotion of their discoveries (I'm referring here to its namer, the influential Henry F. Osborn), was initially studied in one of the world's best funded, most famous museums (the American Museum of Natural History in New York), and was given an awesome name that's fun, and easily remembered and abbreviated to boot. *T. rex* appeared in print in 1905, the original specimen being

one of two—one from Wyoming, one from Montana—discovered by famed fossil-finder and scientist Barnum Brown.

It can also be said that *T. rex* deserves the fame it has. It really is and was an *awesome* animal, a super-powered giant with phenomenal bite strength, an ability to kill and dismember giant prey, and superb sensory abilities. The biggest specimens, like "Sue" of Chicago's Field Museum, are around 13 m (42.6 ft) long and would have weighed between 8 and 14 tonnes (9–15 tons) when alive (estimates differ according to the measurement technique used).

It's easy to see *T. rex* as the culmination of its lineage: as the ultimate final flowering of a long line of predators that became larger, more powerful, and more dedicated to the hunting of giant prey. Osborn and Brown certainly saw *T. rex* that way. Today we think of things as being more complex. *T. rex* and its kin weren't straight-line descendants of earlier big predators (like allosauroids) but had their roots in small coelurosaurs.

Detailed studies involving CT-scanning, computer modeling, and mathematical analyses of many sorts have allowed scientists to work out the muscle size, potential running abilities, eyeball size, hearing abilities, brain anatomy, bite strength, growth rate, and more of this animal. This work—routinely reported by the popular press as well as at academic conferences—makes *T. rex* one of the best understood of non-bird dinosaurs. It had acute vision, smell, and hearing, lived to around 30 years, underwent a massive increase in bulk and robustness during its late teenage years, and was likely an efficient long-distance walker capable of bursts of speed,

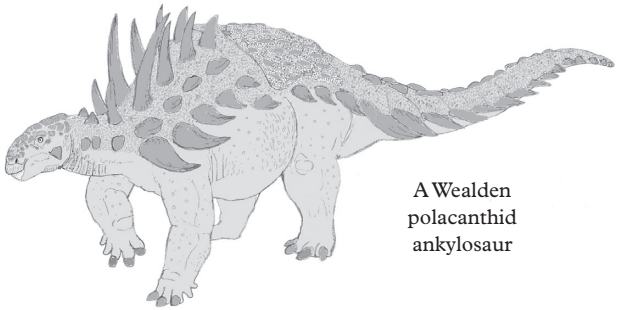
able to kill with phenomenal biting power. Its body was mostly covered in scaly skin but parts of its upper surface may well have had a covering of hairlike feathers. Uncertainty remains over its social life but tracks and the associated skeletons known for its Asian relative *Tarbosaurus* suggest it might have lived in family groups.

The substantial number of *rex*-themed studies that have appeared over the last few decades imply that this animal is over-studied relative to other non-bird dinosaurs. A fairer appraisal would be that its extreme nature—it's one of the biggest bipeds of all time, has among the strongest jaws, biggest teeth, biggest eyes *and so on* of all land-living animals *ever*—make it an inevitable object of study, a "model organism." And its stupendous fame, popularity, and universally known name certainly help when it comes to pitching a funded study.

See also Coelurosaurs; Sue; Tyrannosauroids.

Wealden

A famous Cretaceous series of mudstones, siltstones, and sandstones of southeast England—East Sussex and the Isle of Wight in particular—which yield a historically important fauna of dinosaurs and other fossils. The Wealden (properly, the Wealden Supergroup) incorporates sediments laid down between the Berriasian and early Aptian parts of the Early Cretaceous: that is, between about 145 and 120 million years ago. It includes many subdivisions which reveal numerous environmental changes. Sediments from floodplains, savannas, conifer woodlands, marshes, and lagoons are all represented. Wealden



A Wealden polacanthid ankylosaur

fossils shouldn't be imagined as belonging to a single "Wealden environment" or "Wealden Fauna." Instead, we're talking about a great number of animal and plant communities, living at different times and in different habitats.

Wealden dinosaurs were important in the early history of dinosaur research. Two founding members of Owen's Dinosauria—*Iguanodon* and *Hylaeosaurus*—are from the Wealden, as are remains crucial to early ideas on sauropods and theropods. The Wealden ornithopod *Hypsilophodon*, published in 1869, had a role in linking birds with other dinosaurs.

Exciting finds have also been made in more recent decades. One of the world's best understood spinosaurids—*Baryonyx*—was discovered in the Wealden during the 1980s and an early tyrannosauroid—*Eotyrannus*—was reported from the Wealden in 2001. The presence of rebbachisaurid diplodocoids in the Wealden was established in the early twenty-first century, and the existence of a variety of small theropods has recently been demonstrated thanks to new

microvertebrate studies. At the time of writing, research on Wealden ankylosaurs, spinosaurids, and tyrannosauroids is underway. On that note, there's a substantial literature on Wealden dinosaurs. The ultimate publication is *Dinosaurs of the Isle of Wight*, published by myself and David Martill in 2001.

The majority of the Wealden's dinosaurs come from the Wessex Formation, a mostly Barremian sedimentary unit (dated to between 130 and 125 million years ago) most obviously exposed on the cliffs and coasts of the Isle of Wight's southwest. The ankylosaur *Polacanthus*, the ornithopods *Hypsilophodon* and *Iguanodon*, and the theropods *Neovenator* and *Eotyrannus* come from the Wessex Formation. Dinosaurs from the older parts of the Wealden are less familiar and include the ankylosaur *Hylaeosaurus*, the iguanodontians *Barilium* and *Hypselospinus*, and the mysterious theropods *Altispinax* and *Valdoraptor*.

See also *Iguanodon*; Richard Owen; Spinosaurids.

Zallinger Mural

Among the most famous, influential, and impressive pieces of paleoart, properly called *The Age of Reptiles* mural and on show at Yale's Peabody Museum of Natural History in New Haven, Connecticut. The Zallinger Mural is, first and foremost, a phenomenal piece of art. At 34 m (110 ft) in length, it's among the largest pieces of art in the world. And it's a cultural touchstone, depicting prehistoric life as it was imagined at the time.

The mural owes its existence to the fact that museum director Albert Parr thought the Great Hall barren

and in need of color. Parr asked Lewis York at the Yale School of the Fine Arts if he knew anyone able to create a suitable work of art. York suggested Rudolph F. Zallinger, who was just 23 at the time. After receiving tuition on animal anatomy from paleontologists George Wieland and G. Edward Lewis, Zallinger began the project in 1942, his aim being to create a mural in the fresco secco technique. This is most associated with medieval paintings from Italy and involves mixing pigments with organic binders derived from milk or plant oils. Scaffolding was erected and Zallinger set to work in October 1943. The hall was kept open during the entire time that Zallinger was at work, so his progress was observed by students and the public. He completed it in June 1947.

The mural depicts animal and plant life in the late Paleozoic and Mesozoic, time moving from right to left in keeping with visitor flow through the hall. Conveniently positioned trees mark the boundaries between the geological ages. We start with the swampy, forested world of the Devonian before transitioning to an arid, rocky section populated by *Dimetrodon* and other Permian beasts. Triassic dinosaurs like *Plateosaurus* then appear. Next, things become green and heavily vegetated as Jurassic dinosaurs fill the scene, a great lake-dwelling *Brontosaurus* and arch-backed *Stegosaurus* occupying the mural's middle. Finally, a modern-looking section with a volcanic backdrop shows *Tyrannosaurus* and *Triceratops* moving among magnolias, palms, ginkgos, and willows.

Most reproductions of the mural reverse its orientation such that the image starts on the left. And most

Zallinger's *T. rex*

reproductions depict the miniature prototype, not the actual mural. The miniature—itself proceeded by two pencil-drawn practice illustrations—was painted in egg tempura: a thick, fast-drying pigment tempered with egg yolk. It differs in detail from the mural, especially in the anatomy of the animals. It's actually not easy to find good, detailed photographs of the mural itself—the Peabody seems to restrict its reproduction—and about the only good one available is that included in the Peabody's 1987 book *The Age of Reptiles*, edited by Rosemary Volpe.

Zallinger died in 1995. His son Peter is also a skilled artist who has portrayed prehistoric animals on several

occasions, most notably in John Ostrom's 1986 book *Dinosaurs and Other Archosaurs*.

Zigong Dinosaur Museum

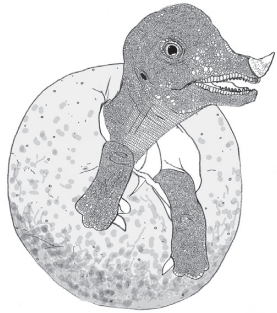
China is home to many spectacular dinosaur-bearing sites, and among the most famous and notable is that preserved as part of the Zigong Dinosaur Museum in Sichuan Province in the country's southwest. Technically, the fossil site is at Dashanpu, a town about 7 km (4.3 miles) from the city of Zigong, but it's the name Zigong that has become most strongly associated with dinosaurs.

The dinosaur wealth of the region was revealed in 1977 during the construction of a quarry created for oil and gas extraction. One of the first finds was a complete skeleton of a sauropod later named *Shunosaurus*. Numerous other discoveries followed, and it became obvious that Dashanpu wasn't just China's and Asia's premiere dinosaur site, it was also globally significant. A series of excavations, involving Chinese paleontologists from several institutions, occurred from 1979 and throughout the 80s. The dinosaurs uncovered by these teams are of Middle and Late Jurassic age and include sauropods (like the spectacularly long-necked *Omeisaurus* and *Mamenchisaurus*), theropods like *Yangchuanosaurus*, and stegosaurs (like *Huayangosaurus*, *Gigantspinosaurus* and *Tuojiangosaurus*).

Many of the Dashanpu fossils went to museums like Beijing's Institute of Vertebrate Paleontology and Paleoanthropology, but there were so many that the construction of a dedicated Zigong Dinosaur Museum was justified. This museum—constructed right

over the quarry—opened in 1987 and remains one of the world's most spectacular dinosaur-themed attractions. It consists of three main sections: a display hall housing mounted skeletons of the site's most spectacular dinosaurs, a series of rooms and balconies that showcase smaller fossils, and the original quarry floor, surrounded by walkways. The building itself is shaped like a symbolic dinosaur. There's the suggestion of four supporting legs, a long, horizontal neck, and a serrated frill along the midline, though it has to be said that the resemblance is very superficial. The museum is a mecca for visiting paleontologists, and it's a highly popular tourist spot as well.

The global significance of Dashanpu's fossil wealth was commemorated in 2008 when it was made part of a UNESCO Global Geopark. Indeed, such is the richness of the area for Jurassic fossils that there's supposed to be more than 14,000 m^2—about 3.5 acres—of dinosaur-bearing rock remaining to be excavated.



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